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SCHARFF'S HISTORY OF THE EUROPEAN FAUNA.

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IN a recent volume of the *Contemporary Science Series*, Dr. Scharff[1] has given us, under the above title, an elaborate attempt to trace the origin of the present fauna of Europe and to some extent also its flora. He has followed up the various migrations which have taken place in that continent chiefly since Pliocene times, and indicated the routes which in his opinion they must have followed, as well as the obstacles which barred their way in other directions. This leads to a discussion of the conditions of climate and distribution of land and water during the glacial epoch. He has thus brought face to face in one volume some of the most important problems in zoölogy, botany, and geology, and whether we agree in his conclusions or not, we owe him a debt of gratitude for the admirable manner in which he has laid the whole question before us and for the mental stimulus which his presentation of it is sure to infuse into the discussion.

[1] Scharff, R. F. The History of the European Fauna. London, Walter Scott, 1899. viii + 364 pp., 8vo, 21 figs. and maps in text.

In the introductory chapter Dr. Scharff, starting out from the present fauna of Great Britain and Ireland, demonstrates its heterogeneous composition, embracing, as it does, animals, the affinities or geological history of which point to their southern, northern, or eastern origin, and shows that in all probability the southern forms must have extended northward from the continent long ages ago, while the others arrived comparatively recently. He then discusses the means of dispersal possessed by the various animals, especially "the occasional means," as Darwin called them, and ventures to think that both Darwin and Wallace have somewhat overestimated its significance, and he reaches the conclusion that five per cent would be a high estimate for the animals which have reached British soil by accidental means. This proportion he regards as insignificant, in fact as utterly negligible.

In the second chapter, which is headed "Preliminary Considerations," Dr. Scharff endeavors to show how to determine approximately the original home of an animal so as to be able to study the component elements of the European fauna. As one of the results he announces that what was formerly believed to have been one great northern invasion now resolves itself into two distinct ones — the Siberian and the Arctic. An examination of the present distribution of mammals, snails, and earthworms shows that the British Islands have been connected with one another and with the continent; Spain with Morocco across the Straits of Gibraltar; Greece with Asia Minor, and so forth. The British fauna forms the key to the solution of the wider problem of that of Europe, five elements being recognizable, of which the Lusitanian is the oldest and the Siberian the most recent. A discussion of the climate of Europe during the glacial period follows, in which Dr. Scharff tries to maintain that so far from being of an Arctic nature the climate was mild, possibly even milder than at present, to which result he is mainly led by a contemplation of the striking and most remarkable mingling of a northern and a southern fauna during the Ice Age. An extensive glaciation, as advocated by modern geologists, is consequently denied and evidence brought forward to demonstrate the marine origin

of the boulder clay as opposed to its character as bottom moraine. Under such climatic conditions portions of the fauna and flora[1] were enabled to continue their existence in localities reached by them in preglacial times.

The British fauna is taken as a convenient starting point and is treated of in the third chapter. Examples are given of the more noteworthy forms belonging to the three foreign elements of which it is composed, *viz.*, the northern, eastern, and southern, as well as a small endemic one, and adhesion given to the almost unanimous opinion of biologists that the bulk of the British fauna and flora (biota? !) is attributable to invasions by land from the continent. As for the relative age of these invasions and the geological periods in which they entered the British Islands, Dr. Scharff feels convinced that the south-western or Lusitanian fauna, and also the flora, must have arrived before the glacial period and survived the latter. The Alpine and Oriental invasions arrived next. After these came the Arctic, and finally the eastern, or Siberian. The geological age of the latter is most easily traced because of the more complete fossil evidence at hand. As the Siberian invasion arrived in Germany after the deposition of the lower boulder clay, consequently after the first portion of the glacial period had passed, it would seem to follow that the Forest Bed in England, which geologists hold to be preglacial, must be interglacial, corresponding to the Loess formation of central Europe. The chapter concludes with statements of facts showing a continuous coast line to have existed between France and Ireland.

With the fourth chapter Dr. Scharff takes up in detail the discussion of what he calls the "Arctic fauna." The basic

[1] The author, like many other writers on similar subjects, has felt the need of a comprehensive term to include both fauna and flora which will not only designate the total of animal and plant life of a given region or period, but also any treatise upon the animals and plants of any geographical area or geological period. As such a term I would suggest *Biota*, not only because its original significance covers the above definition, but also because of its brevity and obvious relationship to the term "Biology" as embracing Zoölogy and Botany. *Biotic* would then signify "pertaining to or treating of a biota," as, — a biotic publication, a biotic region.

supposition upon which rests the whole theory of the Arctic immigration, in so far as such terrestrial animals are concerned, which require a continuous land connection, consists in the assumption that America and Europe were connected far north between Scandinavia, Spitsbergen, and Greenland until toward the end of the glacial period, while Norway again was continuous with Scotland across the North Sea, and England (and Ireland) with France. The earliest traces of such an immigration he finds in certain so-called American plants and fresh-water sponges which are found on the northern and western coasts of Ireland, in the Hebrides, in Scotland, and in North America. "The geographical distribution of some of the Arctic species is referred to in greater detail," to use Dr. Scharff's own words in his summary of this chapter, "to show how the relative age of their entry into Europe can be determined. Two forms of reindeer, resembling the Barren-Ground and Woodland varieties, have been met with in European deposits, but only the former occurs in Ireland and the south of France, whilst eastward the other becomes more common, and finally is the only one found. It is believed that the Barren-Ground is the older form as far as Europe is concerned, and that it came to us with the Arctic migration, and that the other reindeer reached Europe much later from Siberia, when Ireland had already become detached from England. The range of the Arctic hare is equally instructive. It must have been a native of Europe since early glacial or preglacial times — before the common English hare had made its appearance in central Europe. Along with other Arctic forms it entered northern Europe directly from the Arctic regions by means of the former land connection which joined, as I remarked, Lapland with Spitsbergen, Greenland, and North America." The stoat, or ermine, is another distinctly northern animal which Dr. Scharff regards as having reached Ireland and England at two different times; the one from the Arctic regions as a northern migrant, the other with the Siberian fauna from the east, and its range is made to include Greenland and Spitsbergen. He also thinks that there can be no doubt that the British grouse belongs to the northern migration, and the

ptarmigan and snow bunting are also reckoned as invaders from the north. Several other animals are mentioned as Arctic; thus the various lemmings, though it is not quite clear whether he regards these as belonging to the Arctic immigration, since they are also included in the animals constituting the Siberian contingent. The character of the flora is also alluded to as strengthening the theory of an Arctic (*i.e.*, North-America-Greenland-Spitsbergen-Scandinavia-Scotland) route, though a postglacial connection between Europe and Greenland is not insisted on, as the present flora of that country may have survived the glacial period in the Arctic regions. Professor Forbes's opinion, that the occurrence of certain shore Mollusca, both on the coast of Finmark and Greenland, shows that these two countries were not long ago joined, is alluded to, and the view that the continental boulder clay is a marine deposit is again brought forward as fitting so much better with the known facts of distribution.

The Siberian invasion forms the subject of Chapter V, in which a number of British animals, living and extinct, are traced to a Siberian origin, chiefly mammals, and some birds. Among many of the lower vertebrates and invertebrates there are but few species which in Dr. Scharff's opinion have reached England from Siberia. They may have had their original homes in the Alps, in eastern Europe, or in central and southern Asia, and have joined in their westward course the later, more quickly traveling mammals. No less than twenty-six species of the Siberian mammals, according to Scharff, penetrated as far west as the British Islands, and nine of these still inhabit Great Britain. Some of the remaining seventeen species probably lived only for a very short time in England, and the rest gradually became extinct one by one. Our author enumerates them as follows[1]: *Canis lagopus*, *Gulo luscus*, * *Mustela erminea*, * *M. putorius*, * *M. vulgaris*, * *Sorex vulgaris*, *Lagomys pusillus*, * *Castor fiber*, *Spermophilus eversmanni*, *S. erythrogenoides*, *Cricetus songarus*, *Myodes lemmus*, *Cuniculus torquatus*, * *Mus minutus*, * *Arvicola agrestis*, * *A. amphibius*, *A.*

[1] Those marked with an asterisk still inhabit Great Britain, or did so within historic times.

arvalis, * *A. glareolus*, *A. gregalis*, *A. ratticeps*, *Equus caballus*, *Saiga tartarica*, *Ovibos moschatus*, *Alces latifrons*, *A. machlis*, *Rangifer tarandus*. It will be noticed that this list contains species which have also been quoted as Arctic immigrants, in which case, however, Dr. Scharff regards them as having arrived at different times both from the north and from the east. It will also be observed that several species which from their present distribution are regarded as Arctic, — as, for instance, *Canis lagopus* and *Ovibos moschatus*, the Arctic fox and the musk ox, — are given as Siberian immigrants, the latter obviously because it has not been found in Norway, and consequently cannot have come by way of the latter country from Greenland. In discussing the route by which these animals arrived and their origin, Dr. Scharff returns to his *præterea censeo*, that a mild climate prevailed then in central Europe; and in reply to Nehring's "steppe theory" he states that we have really no idea under what precise climatic conditions the Siberian mammals lived in their original home, and offers evidence from other synchronous animals, such as the mollusks, to show that they afford no proof of a steppe character of the country at the time when they were alive. Additional support is derived from the evidence of a connection between the Caspian and the White Sea which would have prevented the Siberian fauna from spreading westward in Pliocene and early glacial times. But on disappearance of the marine connection a way would have been opened into central Europe. The marine character of the boulder clay is again reverted to, and the age of the English Forest Bed determined as interglacial, contemporaneous with the German interglacial beds also containing the bones of these Siberian migrants.

While the so-called Siberian invaders came from the east, they entered Europe by a more northern route than a large number of animals which also came from Asia, but by way of Asia Minor. They compose what Dr. Scharff calls the Oriental migration, which is treated of in detail in Chapter VI, and of which he himself has given the following summary:

"They originated in central, southern, and western Asia. It is not easy to discriminate in all cases between the Oriental

migration and the Siberian. To a certain extent, even an entry of northern Asiatic species has taken place by the southern route, and *vice versa*. On the other hand, southern species might have come to Europe by the southern route — that is to say, to the south of the Caspian — and also by the northern, which lay to the north of that great inland sea. The red deer [*Cervus elaphus*] is a good example. It arrived on our continent by both routes. However, there is a racial difference in the members of the two migrations. The small race now found in Corsica, Sardinia, northwest Africa, and western Europe is probably the older of the two, while the larger one — resembling the American wapiti deer — arrived very much later from Siberia.[1]

"The mammoth, wild boar, badger, the dippers, and pheasants are all Oriental species which have come to us from the southeast; but there are also reptiles and amphibians, and a host of invertebrates. Not all the animals, for instance, which have reached us in England from the southeast are of Asiatic origin. There is an active center of distribution in southeastern Europe itself, from which species radiate out in all directions. This fact is well illustrated by the genus Clausilia. Species from this center, and also from the Alps, joined the Oriental stream in their northward course.

"In reviewing a number of instances of Oriental species in Europe one is struck by the peculiarity of their having apparently followed two distinct routes. All entered from Asia Minor, which is proved to have been connected with Greece until recent geological times. From here some seem to have proceeded straight west, others northward. Further study reveals the fact that the first route was followed by a much older set of migrants at a time when the Mediterranean area was greatly different from what it is at the present day. Greece was then joined to southern Italy, Sicily, and Tunis. The latter was also connected with Sardinia and Corsica, and the Straits of Gibraltar did not exist. Under such geographical

[1] On page 250 it is stated that it appears that it (*i.e.*, the larger race of deer) also reached England. *Cervus elaphus* is not enumerated by Dr. Scharff, however, as one of the Siberian migrants on page 202. — L. S.

conditions a direct migration on land from southern Greece to Spain was not only possible, but was actually undertaken by a very large number of Oriental species."

Chapter VII treats of the Lusitanian fauna in detail. As already mentioned, Dr. Scharff regards this element as the oldest in the British Islands, its antiquity being indicated by the discontinuous distribution of so many of its species. As Lusitanian, he regards species having their origin in the southwestern portions of Europe, "or on the mysterious lands which lay beyond it." Not all the species which have entered Great Britain from that direction, however, are true Lusitanian, inasmuch as many of the Oriental invaders are supposed to have traveled as far as Spain by way of the Mediterranean route, and then, proceeding northward, to have reached France, Ireland, and England. Only one mammal is treated of as undoubted Lusitanian, *viz.*, *Oryctolagus cuniculus*, the rabbit; but several birds are mentioned as having a southwestern origin, prominent among which are the Dartford warbler (*Melizophilus undulatus*), the pied wagtail (*Motacilla lugubris*), and the genus Fringilla. Among the lower vertebrates there are more species of this kind. Thus the ancestors of the amphisbænian lizard (*Blanus cinereus*) are supposed to have entered Europe by way of the sunken "Atlantis"; other probable Lusitanians are the Discoglossoid toads and the salamandine genus Chioglossa. Various butterflies, beetles, and spiders may be similarly traced to a southwestern origin, but especially a large number of land mollusks, notable among which is the spotted slug (*Geomalacus maculosus*), which is known only from Portugal and few localities in southwestern Ireland.

The Alpine fauna forms the subject of the last chapter, the eighth. The history of this part of the fauna begins with the rise of the Alpine island in the Miocene sea. This island, being first connected with the mainland to the east, naturally received its first inhabitants from that direction; and Dr. Scharff regards them as having formed part of the older Oriental invasion, many species of which, by long isolation and the elevation of the Alpine country, became modified into very distinct species, thus forming as it were a new fauna.

At least this is the way I understand Dr. Scharff when he speaks of indigenous Alpine species. Following these came the newer Oriental invasion. During Pliocene times dry land gradually supplanted the sea to the north of the Alps, and their Biota (fauna and flora) poured into the plain. At that period Arctic species from the north (*via* Scandinavia, Great Britain, and France) and Lusitanian forms from the west found their way to the Alps. The true Siberian types came much later, *viz.*, in the Middle Pleistocene, making their appearance at the foot of the Alps, though it is doubtful whether many of them ever reached the mountains. Thus he accounts for the presence of the so-called Scandinavian species in the Alps, and *vice versa*, in two ways — first, an early northern invasion directly from Scandinavia to the Alps *via* England, and, second, by both Scandinavia and the Alps receiving a share of the Siberian colonists, parts of which went north, while others went south. Dr. Scharff is thus led to disagree with Forbes's theory, once quite generally accepted, that this similarity between the mountain faunas of northern and southern Europe was due to a gradual forcing south of the northern species and north of the southern ones by the expanding glaciers on both sides, by their mingling in the intermediate territory and subsequent retreat to their old homes when the glaciers receded, the northern forms mixed with some Alpine species and *vice versa*. Nehring's Tundra theory is also dissented from in so far as it regards the Siberian animals as forming the nucleus of the faunas of these two areas. Dr. Scharff ends the summary of this chapter, and thus the book, with the following remarks: "One of the most important conclusions obtained by this study of the flora in conjunction with the fauna, is that I have emphasised in most of the preceding chapters — *viz.*, that the glacial period in Europe was not a time of extreme cold, and that its destructive effect on the animals and plants was by no means such as is currently believed."

This last sentence is in a measure a clue to Dr. Scharff's whole book, which must be read in the light of it. It must be admitted that he has made out a good case, from the

standpoint of the biologists, against the view that would ascribe to the glacial period so severe a cold and so enormously and universally developed an ice sheet, or ice cap, that all life became extinct and every inch of ground hidden by a thick covering of perpetual ice. I doubt, however, that this is currently believed by the biologists of to-day. I do not think I am much out of the way when I say that most of us regard the conditions and climate of the Ice Age in Europe to have been on the whole much like the conditions and climate of Greenland and the island world north of Hudson Bay at the present time. It would therefore be possible for us to subscribe to Dr. Scharff's conclusion as above worded were it not that in the book itself he goes much farther, requiring, as he does, a climate in central Europe at least as mild as that of the present day or even milder. The present reviewer at least cannot admit that the known facts relative to the distribution of animals and plants during Pliocene and Pleistocene times require such a hypothesis for their satisfactory explanation.

It may be true "that with a comparatively slight change of the atmospheric conditions in the British Islands, we might have glaciers back again on all our highest ranges in England, Scotland, and Ireland" (p. 69), and it may also be true that Falsan, whom Dr. Scharff quotes with evident approval, is right when he says "that the mean annual temperature of France during the glacial period was approximately from 6–9° C., perhaps more. This," Dr. Scharff continues, "is the actual mean annual temperature of the southwest of Sweden and Norway, or the north of Scotland." Of course this statement is correct enough, but the whole question assumes a somewhat different aspect when we consider that the temperature indicated by Falsan means a lowering of the annual temperature of about 5°. This would mean for Berlin a July isotherm like that of Archangelsk; for Berlin and Vienna, a January isotherm like that of the south end of Greenland and an annual isotherm like that for the country between Sitka and the Aliaska peninsula. Under the same conditions Edinburgh would have a summer like the extreme

northern Iceland and Bering Straits and a January temperature like that of Reikiavik.

On page 183 Dr. Scharff makes the following statement: "Everybody knows that northern and Arctic species can live perfectly well in a temperate climate, but that it is almost impossible to acclimatize southern animals in an Arctic or even temperate one. We have in this circumstance almost a proof, therefore, that the climate cannot have been very cold. Though a cold sea bathed the shores of eastern England, and even eventually invaded a portion of northern England, the warm ocean on the west must have effectually prevented any great lowering of temperature." Of course a good deal depends on what we understand by "great." At the period of which Dr. Scharff treats he admits that a cold Arctic current came down along the eastern base of Scandinavia, washing the east coast of England on the west and the northern shore of central Europe on the south. Now, England has even to-day a warm ocean on the west coast; does he imagine that if a cold current — like the Labrador coast current — were to strike the east coast of England the temperature of the British Islands would not be "greatly" lowered? On the two sides of the Atlantic the warm and the cold currents make a difference in the annual temperature of the countries of the same latitude of about 10° C. Such a lowering of the annual temperature in Europe east of Ireland would bring the climate of South Greenland, Labrador, and the Hudson Bay countries to middle England, Holland, central Europe, down to Vienna, the northern edge of the Black Sea, and the northern forth of the Caspian Sea; it would also render Lapland and northern Finland equal to Baffin Land, while the climate of Spitsbergen would be as severe as that of Grinnell Land or both sides of Smith Sound. Under similar conditions France and northern Italy would have the same yearly temperature as Newfoundland, Winnipeg, and the Aliaska peninsula. The conditions which must have prevailed in Germany when land and water were distributed approximately as indicated by Dr. Scharff on his map on page 170 remind one strikingly of a combination of Hudson Bay and Baffin Bay, a combination certainly not

liable to ameliorate the climate which in the adjoining countries cannot have been much different from that of Baffin Land. This conception is of course widely different from an absolutely unbroken ice sheet with a temperature destructive of all higher life, but it is also greatly different from the idea of Dr. Scharff. Moreover, it is not inconsistent with a possibility of even a considerable number of southern forms having survived the glacial period in various sheltered nooks and corners. The humming bird occurs even as far as Sitka, almost in sight of the gigantic glaciers, and forests are known to grow above a substratum of ice. The Lusitanian species in Ireland may well have survived the glacial period, even including the spotted slug (*Geomalacus maculosus*). The fact that it occurs in Cork and Kerry Counties of Ireland to-day does not prove that it lived there throughout the glacial period, and that consequently the glacial climate was mild or milder than now, for on page 156 Dr. Scharff has a chart showing Ireland to have extended probably a couple of hundred miles farther south, this extension forming a large peninsula which must have been washed on both sides by comparatively warm currents. It is quite possible that the more tender species of the Lusitanian fauna enjoyed here a congenial climate during the greatest glaciation, retreating to their present stations in Ireland as the sea rose and the glaciers receded. It is therefore scarcely necessary to postulate a temperate climate for Europe during glacial times. Not only did considerable changes of the climate take place during that period over large areas, but there must of necessity also have been a great variation inside this vast area according to local conditions, while in the adjacent countries not directly subjected to the glaciation these local variations must have been vastly greater. We see even to-day isolated spots having a southern temperature within the limits of countries with a northern climate, and on the other hand similar northern oases in regions bounded by isotherms indicating a southern climate.

One of the principal reasons which has led Dr. Scharff to assume such a mild climate in Europe at that time is the mixture of southern and northern forms in several deposits.

The occurrence of the bones of the hyena, the reindeer, and the hippopotamus in the same caverns at Kirkdale, of the lion and northern voles near Paris, of "the mammoth, the woolly rhinoceros, horse, ox, reindeer, Arctic fox, lemming, and Pica" in the same deposit at Thiede, seems to him ample proof of a southern climate, as he is of the opinion that a northern species can much easier exist in a southern climate than a southern species in a northern one. Dr. Scharff continues (p. 74): "If, in a central European deposit, occurs a mixture of northern and southern forms of animals, the presence of the latter is more remarkable than that of the former. Logically, we should look upon the occurrence of southern species in the north, therefore, as supporting the view that a mild climate had induced them to travel northward." In order to show, however, that this "extraordinary mixture of northern and southern types of animals" is no indication of a warm climate, I will call Dr. Scharff's attention to the fact that we have a striking example even at the present day. It may seem a paradox to many, yet it is a fact that there is a district in eastern Asia where the tiger[1] (which we are used to regard as much a tropical animal as the lion and the rhinoceros) hunts the wild reindeer. That part of Manchuria where this "extraordinary mixture" occurs has an annual temperature of between 0 and $-2°$ C.; in other words, like south Greenland, south Labrador, and central Kamchatka. Surely, this woolly tiger might easily have lived at Thiede during the glacial period at the time of the deposition of the bones of the mammoth, the woolly rhinoceros, etc., and it is just as sure that the presence of its tropical bones in the German deposit would not prove that central Europe then had a subtropical climate.

It seems to me that Dr. Scharff's whole train of reasoning in this matter rests on a misconception. I have above quoted the following axiom of his: "Everybody knows that northern and Arctic species can live perfectly well in a temperate climate, but that it is almost impossible to acclimatize southern animals in an Arctic or even temperate one." On page 74 he

[1] *Felis tigris mongolica* (Lesson).

says: "Breeders of animals and those acquainted with zoölogical gardens know perfectly well that it is much easier to keep a northern species in a southern climate than a southern species in a northern one." Similarly he returns time and again to the curious delicacy of Arctic plants in botanical gardens as a proof that their presence in central Europe during glacial times is no evidence of an Arctic climate. He even adduces the fact that *Dryas octopetala*, one of the most typically Arctic plants, grows wild in profusion on the coast of Galway, in Ireland, at sea level, as strengthening "the view, not only that the Alpine flora is of preglacial origin, but that the climate of Europe during the glacial period was mild."

That the Arctic and Alpine floras survived the glacial period there is but little reason now to doubt, but that conclusion is not inconsistent with an Arctic climate in which all these plants even now flourish. But from this admission to the assumption that the climate was mild is a long cry and the two conclusions are not logically connected. Much less is the inference justified, which Dr. Scharff evidently draws, that the animals and plants which we now find characteristic of the Arctic regions originated during the glacial period during the mild climatic conditions and afterwards were driven off into the Arctic or the Alps by more vigorous invaders from Siberia accommodating themselves to the much severer climate. With regard to the plants, here are Dr. Scharff's own words (p. 239): "This fact [*i.e.*, the difficulty of wintering these plants in the Botanical Gardens] suggests that the Alpine and Arctic plants really did not originate in countries with cold temperatures. They probably made their first appearance long before the glacial period — perhaps in early Tertiary times — chiefly in the Arctic regions, which at that time had a mild climate. They have since become adapted to live in cold countries where they flourish, provided they receive sufficient moisture in the summer, and are protected from severe frost in the winter by a covering of snow." Apart from the fact that this theory is diametrically opposed to his own idea of the difficulty of southern species to accommodate themselves to a northern climate, as expressed above, both views, and in fact the whole

argument, rest upon the fundamentally wrong idea that whole assemblages of species — or single species for that matter — can accommodate themselves to so different conditions without changing their specific identity. Surely the examples which Dr. Scharff mentions, while referring to the difficulty of keeping southern animals and plants alive in northern climates, and, *vice versa*, the greater ease with which northern animals survive in temperate countries, refer to individuals only, though he speaks of species. It is a pretty well established fact by this time that the distribution of an animal or plant (species) is limited within a certain life zone beyond which it cannot proceed with impunity, and that this life zone is bounded by certain isotherms of the propagating season, boundaries which may differ with each species but which are fairly inflexible within the species. This *law*, which Dr. Merriam has so successfully defined and elaborated, renders it certain beyond a doubt that the presence in central Europe of a breeding and propagating assemblage of animals and plants practically identical with that of the Arctic and sub-Arctic regions of to-day indicates a corresponding climate during the propagating season; in other words, the life zone of these Arctic and sub-Arctic species was at some period during the glacial epoch located in central Europe, plants, animals, temperature, and all.

Another reason for Dr. Scharff's adoption of the theory of a mild glacial climate is the alleged marine origin of the boulder clay. Various deposits of marine invertebrate fossils in stratified beds are cited as proof that the boulder clay is not of the nature of a ground moraine. While this question probably is one in which the geologists are more directly concerned, I may say that, in my humble opinion, the most reasonable explanation is that the boulder clay is of a dual origin, — that part of it is deposited on land by the ice sheet, while other portions were formed at the bottom of the sea, dropped by floating ice and bergs. There can be but little doubt that the enormous weight of the Scandinavian ice cap depressed the land to the south of it, so as to bring it under the level of the sea. There was probably always a more or less extensive sea skirting it to the south and east, preceding the glaciers as

they extended southward, following them in their retreat to the north, receiving and distributing the ice floes and icebergs with their deposits in various places according to the varying conditions, such as changes in currents and winds and the oscillations of the rise and fall of the earth's crust. A sea like that, shut out from connection with the Atlantic Ocean to the west, only connecting with the Arctic Sea to the north, and fed by the melting ice and snow of the surrounding countries, would present features something between the Baltic and Hudson Bay. Its waters would naturally be brackish, and consequently deficient in marine life, except in a few favorable localities. The supposition of such a sea would meet all the requirements the biologists can put to it; it would explain the varied conditions of the boulder clay and the presence as well as the scarcity of the distinctly marine deposits. It would also meet their demand for an effective barrier north of the Caspian Sea to the invasion of Siberian forms during the earlier part of the glacial period, as a combination of glacier and sea is as effective for this purpose as either of these agents alone. On the other hand, it certainly cannot be taken as an indication of a mild climate, possibly milder than our present one.

While I have thus been unable to accept one of Dr. Scharff's more general and fundamental propositions, *viz.*, the one which relates to the glacial climate, there is another of his more special conclusions from which I must also dissent, *viz.*, the northern origin of the invasion, which he styles the Arctic migration.

As already explained above, Dr. Scharff accounts for the presence of certain Arctic animals in Ireland, Scotland, and other parts of western Europe, including the Alps and the Pyrenean peninsula, by a supposed immigration from America, *via* a continuous land connection between Greenland, Spitsbergen, Norway, Great Britain and Ireland, and France, this immigration being only subsequent in age to the Lusitanian fauna, and distinctly older than the Siberian immigration, which came to Europe much later from the east, though also consisting, to a great extent, of northern types closely allied to those composing the Arctic invasion.

There is at once a fatal objection to this theory, *viz.*, that there can have been no such land connection during Pliocene or Pleistocene times between Greenland and Spitsbergen. It was formerly generally believed that the Arctic Sea was a fairly uniformly shallow basin, but as one of the most important results of Nansen's *Fram* expedition we know now that the sea north of Spitsbergen and Francis Joseph Land is very deep, certainly more than 1600 fathoms, while to the west of Spitsbergen, between it and Greenland, we have soundings as deep as 2650 fathoms. A wide channel between these countries, certainly not less than 1500 fathoms in depth, connects the North Atlantic deep with the polar basin. It can be said with the utmost certainty that an elevation sufficient to bridge this and thus connect Greenland with Spitsbergen has not existed during the geological periods mentioned.[1] It is highly probable that the extreme elevation in that part of the world at that time did not exceed the present 300-meter line. At all events, there must have been a gap between land and land of at least 150 miles, a distance quite sufficient to bar all migration of the mammalia which Dr. Scharff includes in his Arctic fauna.

But apart from this insuperable barrier, there is a good reason why Spitsbergen cannot have been in the route of these animals, *viz.*, that with one exception they do not occur in Spitsbergen, nor were they ever known to occur there. The Arctic hare is certainly absent, and the records of a lemming and the ermine are highly dubious. Even if it should be true that a lemming occurs there, it is pretty safe to say that it is

[1] It will scarcely do to regard the dead shells of shoal water forms, such as *Yoldia arctica*, which the Danish "Ingolf" expedition in 1896 dredged between Iceland and Jan Mayen Island in depths between 500 and 1300 fathoms, as proof of a corresponding depression since glacial times. It is incredible that these dead shells which are scattered all over the surface of the bottom of the North Atlantic Ocean should have been lying there loose all these thousands or ten thousands of years without being covered up or destroyed. I certainly agree with those who hold that these shells have been dropped there by shore ice floated out to sea. It will be noted, moreover, that even the supposition of an extreme rise of 1300 fathoms does not affect our argument as to the continuity of Greenland and Spitsbergen, since they would still be separated by a deep channel at least 150 miles wide.

Cuniculus torquatus, the presence of which would rather work against Dr. Scharff's theory, since it does not occur in Scandinavia at all. The Spitsbergen reindeer, on the other hand, is so different from the one of Norway that it does not seem probable that one is the lineal descendant of the other. Add to this that the sea between Norway and Spitsbergen is more than 300 meters deep, and an exchange of terrestrial mammals between these two countries becomes highly improbable.

Before proceeding any farther I wish to state that while disagreeing with Dr. Scharff in his supposition of a continuous connection between Greenland and Spitsbergen and between the latter and Norway, over which his Arctic invaders might have traveled, I am in full accord with him in regard to the land bridge between Norway and Great Britain across the North Sea, and also in his conclusion that most of the immigrants which he designates as Arctic belong to an invasion different from and considerably older than the great Siberian immigration. That I also accept the continuity of Great Britain with Ireland and France, the breaking down of this connection between the two former prior to that between England and France, goes without saying; but I do not exactly agree with him in his views as to all the higher vertebrates which he attributes to this invasion.

To any one who is familiar with the present and past distribution of the Norwegian lemming (*Myodes lemmus*[1]) it must be somewhat surprising to find it included by Dr. Scharff among his Siberian colonists, rather than among the Arctic invaders. The reasons are obvious, *viz.*, first, because this rodent does not occur in America and Greenland, whence the Arctic invasion is supposed to have come; second, because it has not as yet been found fossil in Ireland, where, according to the theory, it should have occurred if it a[illegible]ed in Great Britain before the land connection with Irelan[illegible]e down, an event later than the arrival of the Arctic invaders according to Dr. Scharff's chronology. This negative evidence, however, would have been counterbalanced, I imagine, by the fact that remains

[1] I adhere in this review to the nomenclature used by Dr. Scharff without regard to my own preference in the matter, in order to avoid confusion.

belonging to the Norwegian lemming type have lately been discovered in Portugal, since it is one of Dr. Scharff's criteria of a Siberian migrant that it does not occur south of the Alps or Pyrenees, were it not for the impossibility of ascribing an American origin to this species. As I have shown that none of the other Arctics can have come that way, and as the lemming otherwise agrees so well with them in their present and past distribution, I think there can be no difficulty about referring them to the same category.

Nor can I endorse Dr. Scharff's treatment of the various ptarmigans (Lagopus). On page 336 he sums up his conclusions to the effect that "*L. albus* and *L. mutus* appear in our continent chiefly[1] as Arctic migrants." His reason for so regarding the former is given on page 334, where it is stated that "no doubt the British grouse is a descendant of the Scandinavian willow grouse. The latter is known also to inhabit Greenland and Arctic North America, and is even found beyond Bering Straits in northern Siberia." In the first place, as the British grouse (*Lagopus scoticus*), with its brown wing-feathers, is almost certainly nearer the original common ancestor of the willow grouse,[2] it would be the Scandinavian willow grouse (*L. albus*) which must be regarded as the descendant, if there really be a direct line of descent between the two, and not *vice versa*. In the second place, it is easy to show that the geographical distribution of *L. albus* is not that of an Arctic species in Dr. Scharff's sense. It will be noted that he gives Greenland among the localities where this species is found. But it is one of the peculiarities of the distribution of this species that it does not occur in any part of Greenland. It is also absent in Spitsbergen and Iceland, and a route of immigration from America by any one of these countries is consequently out of

[1] On page 334 he regards the latter both as Arctic and Siberian; see also page 142.

[2] The probability that the dark wing color of *L. scoticus* might be the result of reversion is very remote. In a species so variable in its coloring we should in such a case expect a very frequent cropping out of so universal a character immediately and comparatively recently preceding the last change. It must be remembered that the white wing-feathers are characteristic of all the other species and forms of the genus, and that they are not subject to seasonal color changes like the rest of the plumage.

the question. Altogether this species is not found in most of the truly Arctic regions, as it is absent, not only in the above-mentioned islands, but also in Novaya Zemlya, Francis Joseph Land, Taimyr Land north of 72°, New Siberian Islands, Wrangel Land, and the Aleutian Islands. Its northern limit consequently agrees almost exactly with that of the wolverine (Gulo) which Dr. Scharff counts among the Siberian invaders.

With regard to the Tundra ptarmigans (*Lagopus rupestris* and *mutus*) our knowledge is unfortunately not quite so complete, owing to the difficulty of distinguishing correctly between these two forms; but, as Palmén has already indicated, it is highly probable that the latter does not occur east of the White Sea, that in fact it is confined (with its local races) to the Scandinavian mountains with their Lapland spurs, Scotland, the Alps and the Pyrenees, while *L. rupestris* (with its various forms and subspecies) extends over the entire Siberian and North American Tundra and Barren Ground, as well as Spitsbergen, Greenland, and Iceland. The former, therefore, is nearly uniform in its distribution with *Myodes lemmus*, while the latter corresponds fairly well to that of *M. obensis* (and its local forms). The significant fact in this connection, in so far as the ptarmigans are concerned, is that both the Spitsbergen, the Greenland, and the Iceland forms belong to the Siberian and American *L. rupestris*, while the Scandinavian and Scotch (also probably subfossil English and Irish) ptarmigans, with those of Switzerland and the Pyrenees, form the *L. mutus* group. These, therefore, cannot have come from America *via* Greenland and Spitsbergen (or Iceland).

But while thus this group of animals, which Dr. Scharff has called Arctic immigrants, by both physical and distributional reasons is barred from the route America-Greenland-Spitsbergen-Norway-Scotland-western Europe, it may be pertinently asked, By what road did they reach western Europe, Scotland, and Norway?

Let us first determine where they did *not* come from. Having eliminated Greenland and Spitsbergen, there are to the northward only two countries which need be further investigated, *viz.*, Norway and Iceland.

The latter might have been dismissed in a few words, were it not that Dr. Scharff, in his history of the European fauna, practically has no reference to the fauna of Iceland, the origin of which certainly is as European as that of Great Britain itself. Almost the only allusion to the famous island is a brief paragraph to the effect that if a land connection existed between Greenland and Scotland in that direction "it must have been in very early Tertiary times." Granting that there was no such continuous land bridge any more at the beginning of Pleistocene times or even during the Pliocene, by which the larger herbivorous animals could have migrated from Greenland to Iceland and Scotland, it is evident that the conditions must have been much different from what they are indicated to be on Dr. Scharff's diagrammatic maps on pages 156 and 170, in which the present sea level is maintained at Iceland and eastern Greenland, while the continental platform is raised about 200 fathoms at the western coasts of Ireland, Scotland, Norway, and Spitsbergen. Under such a distribution of land and water Iceland, though still an island, must have been much larger, while the Faröe Islands, forming a large island of nearly the present size of Ireland, were separated from Scotland by a comparatively narrow channel, and numerous islets on the high ridge between the Faröe Islands and Iceland constituted a series of stepping-stones to the latter. Such a state of affairs would of course effectually block the way of the mammals, without being a bar to many other animals, as the birds, for instance. To any one familiar with the land birds of Iceland it is perfectly plain that it would require at least that much of an interrupted land connection to make it possible for them to have developed a highly frequented migration route across that now nearly trackless ocean. I will mention only one example, *viz.*, the large-winged race of the common wheatear (*Saxicola œnanthe leucorhoa*). This race, characterized by a length of wing of over 100 mm., is known to breed in Greenland and adjacent portions of northeastern Arctic America and to migrate in winter over Iceland, the Faröe Islands, the Shetlands, Great Britain, and probably thence along the western edge of France and the Pyrenean peninsula to Africa, returning in spring the

same way to its Arctic home. For this bird to have found a way to America there must at the time have existed a route fairly well outlined by islands more extensive and more numerous than now, and the very fact that this route of the extension of its distribution (for it belongs to an exclusively Old-World genus) became an annual migration-route points plainly to the existence of such an interrupted land bridge some time in the glacial period. However, the total absence of the reindeer, the hare, the lemming, the ermine, and the musk ox in Iceland is incontrovertible proof that the Arctic mammalian invasion into western Europe did not come by way of Iceland.

There remains then only Norway as the last possible home of these animals if they arrived from the north at all. The question, however, at once presents itself: If they arrived in Scotland from Norway by way of the North Sea bridge, by what route did they then come into Norway? It is of course out of the question to suppose that they originated in that country situated at the extreme northwest periphery of the Old World, as they are all closely allied to species of arctogæan derivation. On the other hand, there seems to have been no other land connection at that period between Scandinavia and the rest of the Eurasian continent than that with Scotland. It is pretty generally agreed that the sea then covered the lowlands of northern Russia to the east, thus effectually cutting off any communication between Siberia and Lapland. Apart from the considerations which have influenced that conclusion it would be very difficult to explain the absence from the Scandinavian peninsula of a number of both Arctic and Siberian animals had there been a land connection in that region during the earlier and middle stages of the glacial period. The total absence of *Cuniculus torquatus* and the musk ox is particularly significant.

It would then appear that we are compelled to conclude that the mammals and birds in question did not come to Great Britain and Ireland from the north at all. They certainly did not come from the west, and it is equally certain that they formed no part of the Lusitanian fauna. There seems then to be no other way by which they could have reached Englan

and Ireland except over the land connection with France. But how did they get into France? Where did they originally come from? Various reasons preclude any hypothesis of these animals being part of the Oriental invasions, and the offshoot of the later, the Alpine fauna. Their relationships are decidedly Siberian, not central or south Asiatic, and the lemmings, as well as the willow ptarmigan, are quite foreign to the Alps. I have already expressed my agreement with Dr. Scharff that they do not form part of the great later Siberian invasion; they were present in northern Europe long before that event, as shown by their history in the British Islands.

It goes without saying that the relationships of these Arctic animals are decidedly northern and, as already remarked, equally closely Siberian, and I have no doubt that northern and western Siberia was their home, before they invaded western Europe. I am therefore compelled to recognize two distinct Siberian invasions (or rather three, since a third one is in progress to-day) widely separated in time.

The first Siberian invasion (Scharff's Arctic) took place early, probably before the first great glaciation had reached its maximum. Neither ice nor water had yet shut off the passage north of the Caspian Sea and along the northern edge of the central European mountain ranges. Thus the Tundra reindeer, the variable hare, the ermine, the Norwegian lemming, the ptarmigan, the willow grouse, and others penetrated westward to France (and the Pyrenean peninsula) and over the then continuous England, Ireland, and Scotland to western Norway without leaving any traces in the continental boulder clay which was deposited only after they had passed. The maximum of the first glaciation then barred the further ingress of any more Siberians; the boulder clay was deposited next, and on the retreat of the glaciers or rise of the land, — or rather both, — the second Siberian invasion, among which were several of the same species as the first, took place over the boulder clay. It is my impression that the musk ox and the banded lemming (*Cuniculus torquatus*) formed part of the first invasion, but for some reason or other failed to reach sufficiently far west and north early enough to pass into Ireland or Norway. It may

also be questioned whether the willow grouse reached Norway at that time, as such an assumption would involve the dilemma of either regarding *Lagopus scoticus* as a reversion since glacial times or else of supposing the Scandinavian and the present Siberian *Lagopus albus* to have originated independently and yet specifically identically from the brown-winged ancestor, none of which propositions I am at present prepared to accept. To me it appears most probable that *Lagopus scoticus* belongs to the first Siberian invasion reaching Great Britain and Ireland only, but not penetrating to Norway, and that *Lagopus albus*, the white-winged willow grouse, belongs to the second invasion entering Scandinavia from the south. I do not know that anybody has been able to distinguish the bones of these two forms, and it appears most likely to me that the fossil remains which Milne-Edwards records from France and Italy as *L. albus* really belong to *L. scoticus*. The occurrence of the latter south of the Alps is a fairly good indication that it belonged to the first invasion. However that may be, the others must have reached Norway, where they still survive, by the above route, and while the willow grouse, the Norwegian lemming, and the Tundra reindeer died out in central Europe, the remaining species, except the musk ox and Cuniculus, saved themselves in the southern mountain ranges and in congenial parts of Ireland.

It is quite probable that several other species, members of the older Oriental invasion, joined the preglacial Siberian immigration in France. As one of these I regard the red deer of Scotland and Norway, which doubtless forms a small-antlered race, or subspecies, of *Cervus elaphus*. Its distribution in Norway is highly interesting and suggestive, occurring, as it does, only along the western coast from Stavanger up to about Namsos (65° north latitude). It is here confined to the outer coast line, chiefly to the larger islands, while it is entirely absent in the interior or eastern Norway. The deer there, consequently, is restricted to that part of the country lying to the west and north of the backbone of the great ice cap which extended from southwest to northeast across the Scandinavian peninsula during the glacial period. To the south of this ice

divide red deer occur at present only in southern Sweden, but these belong to the great central European race, and it is highly interesting to note that a subfossil antler of this large form also has been found in southeastern Norway, in Ringerike,[1] consequently on the south side of the ice divide. This large-antlered deer, therefore, probably entered the Scandinavian peninsula from the south at a much later period, while the smaller Scotch form came early across the North Sea bridge and settled on the islands off the west coast of Norway. It will be seen that this hypothesis agrees pretty well with Dr. Scharff's views, expressed on page 250, as follows: "There were probably two distinct migrations of the red deer into Europe, an older one coming from Asia Minor into Greece, which stocked Sardinia, Corsica, Malta, and North Africa in the first place, when these were still connected with one another. This same migration likewise affected western continental Europe, the Irish red deer being probably the descendant of this very ancient stock. The latter entered the island when it was still part of the continent. The later migration of a larger form came from Siberia and spread mainly over eastern and central Europe, but it appears that it also reached England, although there is no evidence of any of these Siberian deer having ever inhabited Ireland." It will be seen that the case is exactly parallel to that of the deer in Norway. Dr. Scharff also calls attention in this connection to the double invasion of the reindeer, but under my supposition that both of the latter came from the east the parallelism is still more striking.

One isolated fact appears at first sight to be antagonistic to my theory of western Norway having been invaded from Scotland and not *vice versa*, as Dr. Scharff thinks, *viz.*, the occurrence of a reindeer in Spitsbergen. I have above expressed the opinion that there was not a direct land connection between Spitsbergen and northern Norway at the time when Dr. Scharff's Arctic migration must be supposed to have taken place. Whence then did the Spitsbergen reindeer come from if not from Norway? Unfortunately, the interrelationship of

[1] Collett. *Nyt Mag. Naturv.*, Bd. xxxvi (1898), p. 360.

the various forms, or subspecies, of reindeer is as yet too imperfectly known[1] to permit us to answer this question with any degree of certainty, but I wish to call attention to the fact that the Spitsbergen reindeer (*Rangifer spitzbergensis*) is too different from the typical wild Scandinavian stock to make it probable that the former is a direct descendant from the latter or *vice versa*. On the other hand, the rise of the land in that region 300 meters would still see Norway separated by the sea from Spitsbergen, at the same time leaving the latter connected by dry land with Novaya Zemlya, and there is at present nothing known which would prevent us from assuming that the reindeer originally came to Spitsbergen from Novaya Zemlya and Taimyr Land in Siberia.[2]

In defense and elaboration of his theory of an Arctic migration by way of Arctic America, Greenland, Spitsbergen, Lapland, Dr. Scharff also discusses the travels of the insects and plants and comes to the conclusion that they argue for a land connection along this route. I think it altogether likely that such a dispersal took place, and would even call attention to the fact that the plants along the north coast of Spitsbergen show a greater percentage of Arctic-American plants than those of southern Spitsbergen as corroborative of this theory, but I must insist that an unbroken land connection is not at all necessary for the dispersal of plants and insects along that route, if currents of air and sea were favorable. Dr. Scharff in his preliminary chapter would reduce this kind

[1] If these exceedingly important questions are ever to be solved, it is necessary that they be investigated at once by some competent authority. Not only are the wild reindeer becoming scarce everywhere from excessive hunting, but they are also being mixed up in the various localities to such an extent that extreme care will have to be exercised in using whatever material can now be brought together. Thus in Norway large herds of the Lapland tame reindeer have been located on the southwestern fiells, where they mingle with the wild ones of a possibly different stock; in Spitsbergen also tame Lapland reindeer have become feral, as some of the draft animals which Professor Nordenskiold brought with him from Finmarken ran away; tame Asiatic reindeer have been brought by the thousands across Bering Straits to America, and a herd of Lapland reindeer have also been introduced into Alaska to add to the confusion.

[2] Dr. Scharff in his discussion of the migrations, etc., of the reindeer (pp. 149–158) seems to argue out of the premises that the Barren-Ground reindeer do not occur in Siberia, but this is a mistake.

of dispersal to a minimum because the many happy coincidences necessary for a species to establish itself on a distant shore must be exceedingly rare. But granting this, we must not forget that while the recorded actual observations of direct accidental transplantation and subsequent establishment are few and far between, our entire experience covers scarcely a couple of centuries, while the periods of which we here treat are reckoned in thousands, possibly tens of thousands of years. And how many lucky chances may not have presented themselves in ten thousand years! Moreover, the distances with which we have to do in the present case only look formidable in the Mercator projection, while in reality they probably did not exceed 150 miles. I believe it to be a distinct mistake to suppose that all classes and kinds of animals and plants have followed the same lines of distribution in time and space. As a matter of fact, it may be even said that there are scarcely two species which have exactly the same history. Each one must be worked out separately, and too sweeping generalizations are dangerous at the present state of our knowledge.

It is one of the distinct merits of a book like Dr. Scharff's that it makes plain these defects in our knowledge. It is a kind of stock-taking by which we find out just how our business stands. It must then be admitted with regret that the status is not as satisfactory as one might have reason to expect. There is yet a great uncertainty as to the exact and detailed distribution of many of the larger and more important animals in the Arctic regions and in Europe. The grosser facts are known of course in a general way, but they are not sufficient for the purpose. The finer details are still unknown, or if known in some isolated cases are unavailing because they are as yet only isolated. American mammalogists, for instance, have studied some of the species here treated of in so far as they relate to American forms, but this knowledge is at present a dead one, because the corresponding Asiatic and European forms are still in chaos, or *vice versa*. Dr. Scharff's book shows that there is still much necessary work to be done by the "splitter" of species and subspecies, but it also shows that this work must be done with some purpose in view and

not in the ordinary perfunctory manner for the mere naming and labeling of museum specimens. The time has come when the interrelationship and the sequence in time and space of the various subspecies must be studied. A perusal of *The History of the European Fauna* should make clear to the average describer and namer of animals that his work is only the means to an end. It brings before him the very problems for the solution of which his work is necessary, and the more conscious he becomes of the uses to which it is to be put, the better and more reliable it is apt to be performed.

I do not know whether Dr. Scharff is to be commended or not for having withstood the temptation to correlate the immigration of man into Europe with that of the other post-Pliocene mammals. The wanderings of the plants are alluded to in order to strengthen the views expressed relating to the origin of the fauna. The travels of primitive man must to a great extent have followed much the same lines as the other mammals, the same natural barriers being nearly as effective in his case as in theirs. It might be said that it would require volumes to exhaust this subject alone, but that is almost equally true of all the various groups of animals. Then again it might be objected that our knowledge of the wanderings of prehistoric man in Europe is very limited and uncertain. I think, however, it can be safely asserted that it is not any more so than our knowledge of the migrations of the animals and plants in the same period, and I venture to suggest that there is a remarkable similarity between the migrations we have discussed above and those of the various European subspecies of man.

The first point to be observed is that the dolichocephalic brunet Mediterranean, or Atlanto-Mediterranean, race in its distribution both in time and space clearly corresponds to Dr. Scharff's "Lusitanian fauna." The agreement is not only a general one, but in some details almost startling, as seen if one compares, for instance, Scharff's map on page 7 with any map showing the distribution of the brunet type in the British Islands.

The next point is the almost self-evident absence of an "Arctic immigration" by way of Greenland-Spitsbergen-Norway-British Islands. On the other hand, the "Alpine fauna," the offshoot of the Oriental immigration, is plainly represented by the brachycephalic Alpine race of unmistakable Asiatic relationship. These "round-barrow men" in their westward push reached the British Islands, though they have left but few traces, except their bones, behind them there. Ireland may have been separated at the time of their invasion, since they do not seem to have reached that island, but they penetrated to the extreme of Scotland, the Shetlands, the Faröe Islands, and, as I believe, by that route — the North Sea bridge, either yet intact or only broken to the extent of furnishing stepping-stones — to western Norway, where to the present day this Alpine population holds the extreme west coast to almost the identical extent as the red deer, a most suggestive distribution when we compare it with what has been said above about the probable route of immigration of that animal in Norway. It is true that there are traces of an Alpine population in other parts of southern Norway, especially in Smaalenene, and that a migration along the Danish peninsula has been suggested. It is even likely that part of the broad-headed dark Norwegians have come by the latter route as well, but this view is not necessarily antagonistic to the above theory.

Finally the long-headed blond Nordic, or Teutonic, race, the last to arrive, corresponds substantially to the "Siberian invasion."[1] Whether any part of this can be paralleled with the preglacial, or first, Siberian stream which I have indicated above, I am not now prepared to say, but the question should be carefully looked into.

[1] This view does not antagonize the theory of the African origin of the dolichocephalic race. On the contrary, I hold that the portion of the latter which ultimately developed into the blond branch originally expanded from eastern Africa to western and central Asia. Here, in the high altitudes, I take it, the bleaching began, which after the race joined the second Siberian invasion, became more and more pronounced as it progressed westward and northward, until it reached its extreme development of blondness at the extreme northwestern point of its range, *viz.*, in Sweden.

It will be seen that Dr. Scharff's book has tempted me even beyond its own limits. This suggestiveness must serve not only as an excuse for this transgression, but also for the length of this review. It is one of the greatest merits of the book.

UNITED STATES NATIONAL MUSEUM.

ON THE QUESTION OF AN ARBOREAL ANCESTRY OF THE MARSUPIALIA, AND THE INTER-RELATIONSHIPS OF THE MAMMALIAN SUBCLASSES.

A REVIEW OF CERTAIN PHASES OF PRESENT AND PAST OPINION.

B. ARTHUR BENSLEY.

RECENT researches have seemed to indicate that the theory, proposed by Huxley, of a genetic succession of the former representatives of the Monotremata, Marsupialia, and Placentalia, is untenable, and have thus reopened the most fundamental question of mammalian zoölogy, as to the interrelationships of the primary subclasses and the possibility of a di- or polyphyletic origin.

The recent publication by Dollo ('99) of the results of his studies on the foot structure of the Marsupialia, which he interprets as confirming the growing idea of a placental origin of the group, renders this an opportune time to review and comment upon certain features of the evidence which has lately been produced in opposition to Huxley's theory.

I. THE EVIDENCE OF AN ARBOREAL ANCESTRY OF THE MARSUPIALIA AND ITS BEARING AS INTERPRETED BY DOLLO.

The question of arboreal ancestry is of considerable importance in determining the relationships of the Marsupialia, and Dollo's results may accordingly be reviewed in some detail.

On page 191 of his paper we find the problem involved set forth as follows:

"Car si cette étude démontre que les ancêtres immédiats des Marsupiaux étaient arboricoles, il sera prouvé, du même coup, que ces Mammifères ne peuvent représenter la souche des Placentaires.

"En effet, personne ne soutiendra que *tous* ceux ci ont passé par une phase arboricole. Et quant à ceux qui en sont là aujourd'hui, ce sont des types sporadiques, qui ont pris naissance indépendamment: la chose est évidente.

"Si, donc, la nature du pied des Marsupiaux nous amène à ce résultat, que leurs ancêtres immédiats étaient arboricoles, cette conclusion contribuera à appuyer ce que nous ont appris le placenta et la dentition du lait, notamment:

"A savoir, que les Marsupiaux constituent un rameau latéral très specialisé, et non le groupe générateur des Euthériens actuels."

The essential element of Dollo's theme is therefore an attempt to prove, by means of the structure of the foot, that the Marsupialia are primarily arboreal animals and that in respect to the possession of an arboreally modified foot they are too specialized to have constituted the source of the Placentalia.

Dollo recognizes in the marsupial hind foot certain characters of arboreal adaptation. These are (*a*) opposability of the hallux, (*b*) predominance of the fourth digit, with reduction and syndactylism of the second and third, and (*c*) recession of the claws. These characters represent successive stages in the development and perfection of a prehensile foot. Their purpose is essentially that of placing the great toe in opposition to the outer digits, notably the fourth, in order to make the foot an efficient organ for grasping and holding fast to the limbs of trees.

For convenience Dollo considers the marsupials in two series, — those which have the great toe well developed and functional, and those which have it reduced, or atrophied. This division is naturally one of habit; the former are animals which have retained the arboreal habit, while the latter are animals which have abandoned it. In these the great toe, being no longer useful, has become reduced.

To the first series belong the American opossums (Didelphyidæ) and the Australian phalangers (Phalangeridæ). In the Didelphyidæ (Fig. 1, *a*), with the exception of the subgenera Micoureus and Philander, opposability of the hallux is

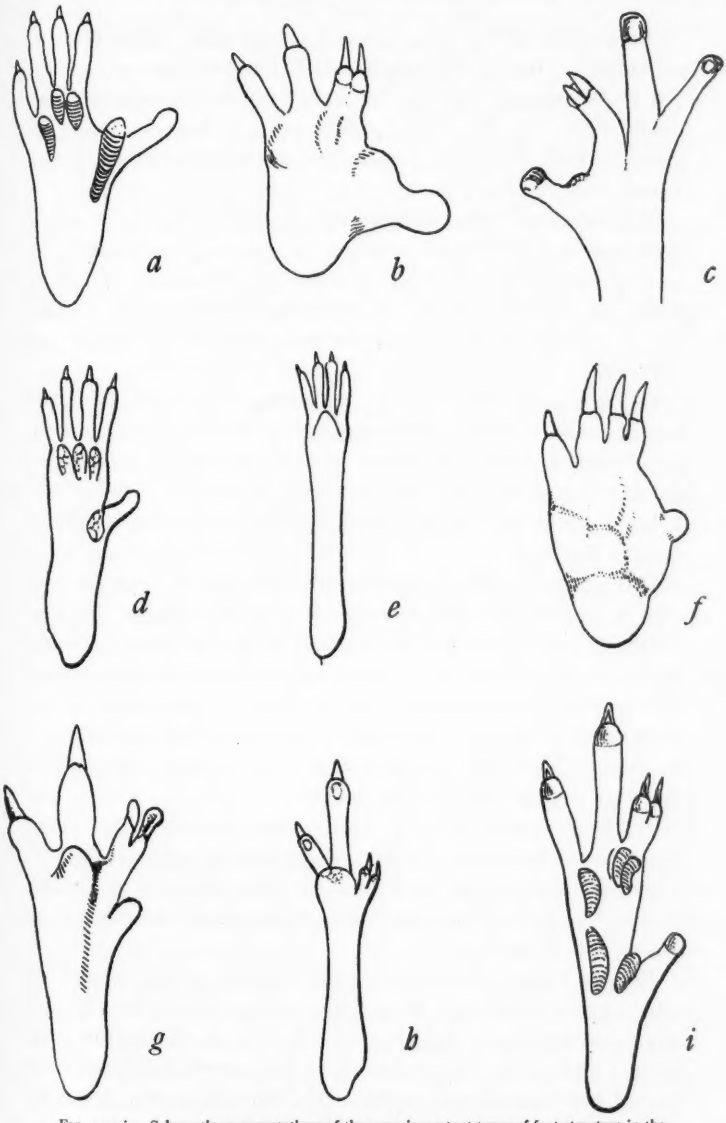


FIG. 1, *a–i*. — Schematic representations of the more important types of foot structure in the Marsupialia, as interpreted by Dollo.

a, Didelphys nudicaudata; b, Phalanger celebensis; c, Tarsipes rostratus; d, Sminthopsis murina; e, Antechinomys laniger; f, Phascolomys ursinus; g, Perameles doreyana; h, Peragal eleucura; i, Hypsiprymnodon moschatus. (After Dollo.) For explanation see text.

the only arboreal character presented, the other digits remaining normal. But in Micoureus and Philander there is, in addition to the opposability of the hallux, an enlargement of the fourth digit. In the Phalangeridæ (Fig. 1, *b*) there is superadded to both of these a reduction and syndactylism of the second and third digits.

One member of the Phalangeridæ, Tarsipes (Fig. 1, *c*), which is unique in many other respects, is the only marsupial presenting the latest stage of arboreal modification. Tarsipes shows, in addition to all of the arboreal characters of the typical phalangers, a recession of the claws of the fourth and fifth digits.

To the second series belong the remaining members of the Australian fauna, the dasyures and their relatives (Dasyuridæ), the wombats (Phascolomyidæ), the bandicoots (Peramelidæ), and the kangaroos and wallabies (Macropodidæ). These animals are mainly terrestrial, but they all show arboreal modifications of the foot.

The dasyures have a functionally tetradactyl foot, derived from a pentadactyl one by reduction of the hallux. Various stages of this reduction are illustrated in the family; *Sminthopsis murina* (Fig. 1, *d*), for example, shows a well-formed hallux, while *Antechinomys laniger* (Fig. 1, *e*) has none at all. Wherever the hallux is indicated, however, it is of the opposable type. As in the Didelphyidæ, this is the only arboreal character represented in the family.

In the wombats (Fig. 1, *f*) arboreal characters are more numerous. The hallux is here reduced to a tubercle, but its transverse position proves it to have been formerly opposable. In addition, there is a slight syndactylism and reduction of the second and third digits.

The bandicoots have a functionally monodactyl foot, derived from a pentadactyl one by an enlargement of the fourth digit and a corresponding reduction of the others, notably the first, second, and third. It shows all of the arboreal characters of that of the typical phalangers. The least departure from the phalangerine condition is seen in *Perameles doreyana* (Fig. 1, *g*), in which the only pronounced modification is a reduction of the

hallux. The greatest departure from this condition is seen in *Peragale leucura* (Fig. 1, *h*) and in *Chœropus castanotis*, in both of which the hallux is entirely obliterated, the fourth digit greatly enlarged, and the remaining digits much reduced.

The exclusive predominance of the fourth digit in Chœropus Dollo regards as significant evidence of former arboreal habit, since in other cases in which there is a tendency towards monodactylism, as, for example, in the horse, it is not the fourth digit which predominates, but the third. The fourth digit must have been enlarged, and the third reduced, in the Peramelidæ, in connection with arboreal habit, before the tendency towards monodactylism appeared in connection with terrestrial, cursorial habit; so that the already enlarged fourth digit became still more predominant, while the third became still more reduced.

The kangaroos and wallabies also have a functionally monodactyl foot, resembling closely that of the bandicoots, and showing a similar range of modification. The musk-kangaroo (*Hypsiprymnodon moschatus*) (Fig. 1, *i*), for example, which is the most generalized type of the family, has a foot which, like that of *Perameles doreyana*, is but little modified away from the phalangerine condition. The true kangaroos, on the other hand, have an extreme monodactyl foot, like that of the higher bandicoots.

Dollo considers separately the South American form Cœnolestes (Epanorthidæ) and the Australian burrowing form Notoryctes (Notoryctidæ). With regard to the former he quotes the description of the foot given by Thomas, as "hallux short, clawless, and not properly opposable; other digits subequal, the fourth slightly the longest." He recognizes this case as doubtful, but thinks it entirely probable that Cœnolestes also is of arboreal derivation.

In Notoryctes, finally, he finds indicated predominance of the fourth digit, and reduction and syndactylism of the second and third. These characters, he states, have not been adaptively developed in connection with a burrowing habit because they are not found in other burrowing animals, such as the moles (Talpa and Chrysochloris). They point rather to a former arboreal habit.

Dollo accordingly finds in all of the Marsupialia examined a more or less extensive arboreal modification of the foot, and from this he draws the following conclusions:

All of the Marsupialia were at one time arboreal.

In the possession of a modified foot they are too specialized to have constituted the source of the Placentalia.

They are, on the other hand, *highly modified Placentalia, in which the placenta has been lost.*

They doubtless arose from *very primitive Placentalia, in which an imperfect placentation resulted in frequent accidents, such as premature birth, and it was probably to avoid these accidents that the placenta disappeared.*

According to this conception there would be four types of development in the Mammalia, as follows: (1) An oviparous condition in the Monotremata, and formerly in the Prototheria. (2) A viviparous condition, *in which the placenta has not yet appeared; found in none of the existing forms*, but formerly present in the Metatheria. (3) A viviparous condition, with placenta, in the Placentalia, and formerly in the Eutheria. (4) A viviparous condition, *in which the placenta has disappeared, in the Marsupialia.*

II. HUXLEY'S HYPOTHESIS IN THE LIGHT OF RECENT RESEARCHES.

In order to define clearly the position of Dollo and other investigators on the question of the relationships of the Mammalia, it is necessary to notice in some detail the view of Huxley as expressed in his famous paper of 1880, with which modern speculation on this subject may be said to have begun.

Huxley recognized three primary and, in a sense, hypothetical divisions of the Mammalia, which he designated as Prototheria, Metatheria, and Eutheria, these groups being represented at the present day by the Monotremata, Marsupialia, and Placentalia, respectively. The existing Monotremata and Marsupialia he regarded as highly modified away from their original types, but the most generalized of the existing Placentalia (Insectivora) as only slightly so. He

recognized a genetic succession of Prototheria, Metatheria, and Eutheria, the Metatheria being intermediate with respect to the possession of certain prototherian and certain eutherian characters, among the former notably a non-placental allantois. To the Marsupialia, in passing from the purely metatherian condition, he assigned the adoption of the following special characters: a prehensile foot, associated with arboreal habit; a marsupium; a reduced milk dentition; a foreshortened period of uterogestation.

Huxley therefore implied the following plan of succession: the Prototheria giving rise to the Metatheria, and becoming specialized as Monotremata; the Metatheria, in turn, giving rise to the Eutheria, and becoming specialized as Marsupialia; the Eutheria becoming specialized as Placentalia.

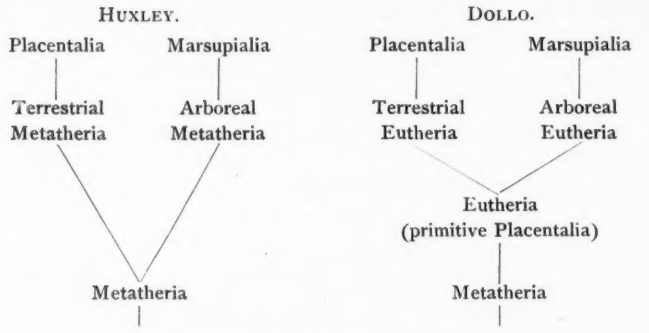
In opposition to this Dollo and others regard the Metatheria as giving rise to the Eutheria or primitive Placentalia, and the latter as giving rise, on the one hand, by retention of the placenta, to the modern Placentalia, and, on the other, by loss of the placenta, to the Marsupialia. Other investigators, notably Osborn, Hubrecht, and Seeley, recognize a separate origin of the main mammalian stems.

With this introduction we may examine certain features of the evidence on which these views are based.

1. *The Question of a Placental Origin of the Marsupialia.*

In the first place, what is the bearing of arboreal ancestry?

If we assign to arboreal habit any value as a differential character of the Mammalia, we may recognize two possible arrangements, based on the views of Huxley and Dollo, in which this factor might appear. For the sake of clearness these may be indicated in tabular form as on following page. According to the former plan arboreal habit would be associated with the differentiation of the Marsupialia and Placentalia. According to the latter it would also be an index — following Dollo — of a placental (eutherian) origin of the Marsupialia. This will make it clear that we have two distinct problems to decide: one as to the value of arboreal ancestry



as an index of a placental origin of marsupials, the other as to its value as a factor of differentiation of marsupials and placentals.

For the solution of the former we have not far to seek. We may at once accept Dollo's statement that the ancestors of the Marsupialia were, in the possession of a modified foot, too specialized to have given rise to the Placentalia, because it is impossible to make any other assumption. In doing so, however, we do not in any way compromise Huxley's view; for it must be remembered that Huxley derived the Placentalia, not from Marsupialia, but from Metatheria. The prehensile foot he regarded as a special marsupial character. On the other hand, we cannot accept the evidence of arboreal ancestry as indicating a placental origin of marsupials. It scarcely needs to be observed that the assumption by non-placental Metatheria of an arboreal habit would account for, and in as satisfactory a way, the arboreal modifications of the foot which Dollo has demonstrated throughout the existing forms.

The latter problem yields much more satisfactory results. It is on this account, in fact, that Dollo's results have been considered in detail. If the former existence of an arboreal habit throughout the Marsupialia were susceptible of decisive proof,[1] we would have a fairly reliable index of the cause of the

[1] I would regard the present evidence of arboreal ancestry as suggestive rather than as conclusive. Dollo has demonstrated conclusively that the Australian Marsupialia are of arboreal derivation, but a study of their characters, notably those of the teeth and feet, convinces me that they have arisen by a rapid adaptive radiation from opossum-like ancestors. If such is the case, they are not at

original separation of marsupials and placentals, because on a basis of arboreal habit we can explain the more important of the special characters which now distinguish the former. It is of interest to notice in this connection the opinion of Huxley: "I think it probable, from the character of the pes, that the primitive forms, whence the existing Marsupialia have been derived, were arboreal animals; and it is not difficult, I conceive, to see that, with such habits, it may have been highly advantageous to an animal to get rid of its young from the interior of its body at as early a period of development as possible, and to supply it with nourishment during the later periods through the lacteal glands, rather than through an imperfect form of placenta."[1] In other words, Huxley regarded arboreal habit as explaining two important characters of marsupials, namely the prehensile foot and premature birth. Now to these we may safely add the reduction of one of the dentitions, because, as Leche[2] has indicated, this is probably attributable to the peculiar suckling conditions which are brought about by premature birth. We may also add the marsupium; Klaatsch ('92) has shown that the perfect marsupium is a special character of the Marsupialia, and its perfect development in this group may best be explained on a basis of arboreal habit. Naturally these suggestions cannot be regarded as at all final, but they point strongly to an association of the special characters of marsupials with arboreal habit.

Passing by the results of Dollo, we find the idea of a placental origin of marsupials also expressed by Wilson and Hill ('97). These writers, in fact, originated this conception and produced what is perhaps the most significant evidence in its favor.

The valuable joint contribution of Wilson and Hill ('97) on the tooth development of Perameles, published in 1897, tended to confirm the idea, conceived by Huxley ('80), but elaborated

all representative of the Marsupialia in general. In the Jurassic fauna of the northern hemisphere, and the Miocene fauna of diprotodonts of South America, we have two important groups for which an arboreal habit cannot as yet be proven.

[1] Huxley ('80, p. 656).

[2] Leche. *Morph. Jahrb.*, Bd. xix, p. 525.

notably by Röse and Kükenthal,[1] of the former existence of a complete double dentition in the Marsupialia, and also indicated their tooth series as directly comparable to those of the Placentalia. Prior to this the permanent antemolar series of marsupials had been regarded as homologous not with the permanent series of placentals but with their milk series.[2] The results of Wilson and Hill seemed accordingly to suggest a fundamental relationship between the two groups in respect to dentition.

Similarly, the brilliant discovery by Hill ('97) of an allantoic placenta in Perameles, which was announced at about the same time, appeared to indicate a further relationship in respect to placentation, the Marsupialia having been previously regarded as entirely non-placental.

These writers in discussing the bearing of their results, although maintaining a moderate position throughout, recognized these resemblances as primary, and indicated their preference for a derivation of the Marsupialia, by retrogression both of milk dentition and placenta, from primitive Placentalia.

Now, although it must be admitted that decisive proof of a former diphyodont condition in the Marsupialia would be of considerable confirmatory value in the presence of other evidence, it would not of itself suggest placental origin. The possibility of such a condition was clearly perceived by Huxley in advocating the reverse. On page 655 of his essay he says: "I think that there can be no reasonable doubt that the existing marsupials have undergone a like suppression of the deciduous teeth, in the course of their derivation from ancestors which possessed a full set." Huxley, in fact, astutely realized that, in order to successfully derive the Marsupialia and Placentalia, it was necessary to assume the existence of a diphyodont condition in their metatherian ancestors.

We may accordingly pass over the evidence derivable from the tooth development of Perameles and consider in detail only that presented by Hill alone from a study of the placenta of

[1] See Wilson and Hill ('97, pp. 433–438).

[2] Röse, Kükenthal, Leche; see Wilson and Hill ('97, p. 582). This view has been recently supported by Dependorf ('98).

this animal and the modifications of the allantois in other marsupials.

Prior to Hill's discovery of the placental allantois of Perameles, other investigators [1] had examined the modifications of the allantois in certain other forms. Owen, Selenka, and Semon had described for the phalangers (Phalangeridæ) and kangaroos (Macropodidæ) (Fig. 2, *c*) one condition in which the allantois was reduced and enclosed by the yolk-sac. Selenka had found a similar condition in the opossum (Didelphyidæ). Caldwell and Semon, on the other hand, had found in the koala (Phascolarctos) (Fig. 2, *b*) another condition in which

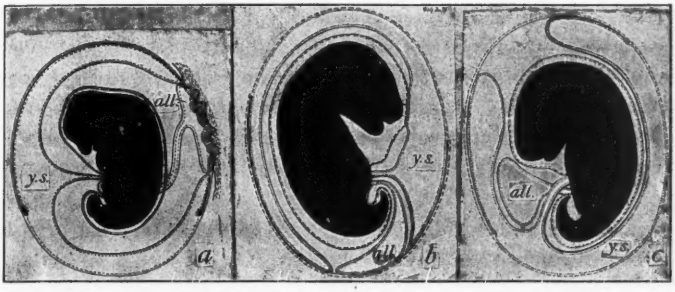


FIG. 2, *a–c*.—The main modifications of the marsupial allantois arranged in the order of their primitiveness as interpreted by Hill. (*b* may represent the type from which *a* and *c* have been derived.)

a, placental allantois of Perameles (from Parker and Haswell, after Hill); *b*, "respiratory" allantois of *Phascolarctos cinereus*; *c*, the reduced allantois of *Æpyprymnus rufescens* (Macropodidæ), (*b* and *c* after Semon); *y.s.*, yolk-sac; *all.*, allantois.

the allantois was well developed and freely exposed to contact with the embryonic envelope, much as in the Reptilia.

In his concluding remarks Hill considers these types and endeavors to decide as to which one of them is the most primitive; in other words, to determine whether a placental allantois is being developed secondarily in the Marsupialia, or whether the placental condition was formerly present throughout the group and has been subsequently lost in all forms (so far as known) but one.

He argues thus: that the reduced condition of the allantois is necessarily secondary; that although it is possible to derive

[1] See Hill ('**97**, p. 438).

the placental allantois of Perameles from one of non-placental type, like that of Phascolarctos, the reverse procedure is the more natural one, because Perameles is of more archaic aspect than Phascolarctos, and the latter is much more retrogressive in dentition; that it is entirely improbable that such a structure as an allantoic placenta should have developed twice independently in the Mammalia (*i.e.*, independently in Perameles). On these grounds he would regard the placental condition of the allantois as the primitive one for the Marsupialia and the non-placental allantois of most existing forms as secondarily derived by retrogression.

That the typical condition of the allantois has arisen by reduction, and is therefore secondary, naturally admits of no reasonable doubt, for no one would suppose that the allantois would be incipient in animals which have passed through an oviparous phase. That the evidence derivable from the organization of the Marsupialia may be interpreted as proving a reduction of the allantois from a placental to a non-placental condition is, however, open to objection, both on general and on special grounds. In opposition we may maintain that there is no possible, and at the same time legitimate, way of assuming retrogression of the allantois on a basis of retrogression in other structures, especially those of adaptive character.

On general grounds, changes in the embryonic membranes may not be closely correlated with adaptive changes (progressive or otherwise) in the general organization. For example, the modifications of the placenta in placental mammals are not directly related to the adaptive (ordinal) characters of the animals in which they occur; several modifications may occur in the same group (*e.g.*, Edentata), a condition which may possibly be due, as Hubrecht[1] has suggested, to the greater youth of the placenta as compared with other structures of the animal organization, but which is more probably due to the fact that the allantoic placenta is not directly affected by the various evolutionary factors which determine the appearance of adaptive characters in the animal.

But even admitting such a correlation, retrogression of

[1] Hubrecht (**'89**, p. 388).

placenta could not be assumed on a basis of retrogression in single structures. For example, if we assume retrogression of the allantois from a placental to a non-placental condition on a basis of the more retrogressive character of the teeth of Phascolarctos as compared with those of Perameles, as suggested by Hill, we may also assume the reverse on the evidence of the feet, for, as Dollo has shown, the foot type of Perameles is a direct natural advance on that of Phascolarctos.

The greatest objection, however, might be taken on the special grounds that the reduction and modification of the teeth which has taken place in Phascolarctos is not retrogressive ("decadent," Hill, p. 435) at all, but is, on the other hand, progressive and very comparable to that which has taken place in ungulate placentals; and, further, that as far as the greater primitiveness of Perameles or Phascolarctos is concerned there is little to choose, for although the former is decidedly more archaic in general dentition, its individual upper molar teeth are well evolved (quadritubercular), and its foot is much more specialized.

In all, it may be said that efforts to explain the reduction of the allantois, whether from a placental or non-placental condition, by reference to retrogression of the general organization are foredoomed to failure; for whatever may be true of the Marsupialia in general, the Australian members of the group, far from being degenerate, show a progressive adaptive radiation (doubtless made possible through freedom from competition) which parallels, and is in general very comparable to that which has taken place during the Tertiary period in placental mammals.

And in view of this a parallelism of placenta, though not genetically related to them, need not be more surprising than the extensive parallelisms in other structures. In other words, there is no adequate reason why the placental allantois of Perameles should not be regarded as *having arisen by progressive modification from one of non-placental (sauropsidan) type.*

These suggestions naturally do not imply that the placenta of Perameles is not primitive, or that in general the reduced allantois of the Marsupialia has not degraded from one of

placental type, but that, as far as present evidence goes, the alternative view is just as plausible

The question now to be decided is whether or not the latter explains the facts of the case equally well.

Admitting the reduced allantois to be secondary, and recognizing the importance of the yolk-sac stage in marsupials, is it not just as probable that the reduced allantois has proceeded from one of sauropsidan type as that it has proceeded from one of placental type? A failure, due to whatever cause, of the allantois to form a placental connection furnishes a more plausible explanation of the premature birth of marsupials than that of Dollo ('99, p. 203), which attributes it to the loss of placenta in the violent gymnastics of an arboreal life. And it thus affords a simple explanation of the reduction of the allantois, inasmuch as premature birth, instituted through the failure of the allantois to form a placental connection, provides not only for the nutrition of the embryo but also for its respiration. This condition being perfected, the allantois, which is a provision for respiration during the later embryonic stages, having its function usurped, has naturally become reduced.

Why the allantois should have failed to form a placental connection cannot at present be explained. The question naturally suggests itself, Is not this also attributable to arboreal habit? It is not improbable that there may have been something in the assumption by metatherian animals of an arboreal habit which, for mechanical reasons, may have made a placental formation impossible.

While still concerned with the former relationships of marsupials, it is of interest to notice certain facts concerning their ancestry which have been derived from paleontology.

In a recent paper on the origin of mammals, Osborn ('99) has dealt with this subject and has represented in the form of a chart the probable geological and phylogenetic relationships of the mammalian subclasses. In this the Prototheria and Eutheria[1] are depicted as primary groups in the Triassic, the

[1] Following Gill's division of 1872 (*cf.* Gill, '72). The Eutheria as defined by Gill are not assigned a placental or non-placental character. Hence they may be interpreted as equivalent either to the Metatheria of Huxley or to his Eutheria as interpreted by Wilson, Hill, and Dollo.

former appearing at a slightly later period than the latter. The Eutheria are depicted as giving rise, somewhere in the upper part of the Triassic, to the Marsupialia and Placentalia, which are represented in the Jurassic by the Triconodonta and Insectivora primitiva, respectively. The significant feature of this is the time relation which is implied by the recognition of marsupial and placental types among the Jurassic Mammalia.[1] If we may argue from the probable sequence of events, it would appear that we have an important clue to the characters of the Jurassic forms, namely the single tooth change of Triconodon, providing that the latter is comparable to that of existing forms. For if the reduction of one dentition is, as Leche suggests, attributable to premature birth, and the latter is, as Huxley and Dollo suggest, in turn dependent upon arboreal habit, then already in the Jurassic period the marsupials must have had their special characters well under way; so that the common ancestors of marsupials and placentals must be placed, as Osborn has indicated, at some time prior to the Jurassic period. Naturally this gives us no clue to a placental or non-placental origin of marsupials, but the distinction, if valid, is an important one, because it avoids the confusion which would result from an attempt to identify and characterize the common ancestors among the more complex faunas of later periods. But more especially it minimizes the importance of the arboreal characters of the marsupials of later periods and renders necessary a knowledge of the foot structure of Jurassic forms before decisive proof of arboreal ancestry may be obtained.

2. *The Question of a Polyphyletic Origin of the Mammalia.*

As indicated above, the view of Dollo, Wilson, and Hill opposes that of Huxley merely in reversing the relationships of marsupials and placentals while retaining the idea of a general continuity of the Mammalia. The views of other writers, on the other hand, substitute for continuity an independent origin and development of the main mammalian stems.

[1] Proposed in 1888; *cf.* opposite opinion of Flower and Lydekker ('**91**, p. 113).

Among the latter there is notably that of Hubrecht ('95), which recognizes a polyphyletic origin of the Mammalia from viviparous Amphibia.

Whether or not the embryological data on which Hubrecht bases his conclusions justify this interpretation is a question on which the writer does not feel competent to express an opinion. It may be noticed, however, that Hubrecht's results are differently interpreted by Assheton ('98), and that his hypothesis has not been generally accepted.[1]

Hubrecht cites in support of his hypothesis the results of Gegenbaur ('86), Mivart ('88), Osborn ('93), and Klaatsch ('92). These may accordingly be examined at the same time in relation to the view of Hubrecht and that of Huxley.

In the first place, Hubrecht regards the recognition by Gegenbaur and Mivart of a fundamental difference between the mammary glands of monotremes and those of the higher mammals as implying an independent origin of the two groups. In some respects this is open to a different interpretation. Gegenbaur, while emphasizing the sudoriparous nature of the mammary glands of monotremes as opposed to the sebaceous nature of those of the higher mammals, was fully aware of the limitations of this distinction, since he found on the mammary areas of monotremes some glands of the latter kind. In discussing the bearing of this he says (p. 35): "Aus solchen Verhältnissen des Drüsenfeldes kann man die Entstehung der Mammardrüsen bei Monotremen und den übrigen Säugern sich vorstellen. Bei den Einen ist die eine Drüsenart, bei den Anderen die andere zur Ausbildung gelangt." In other words, he perceived that from a diffuse condition, in which both kinds of glands were present, we may derive the monotreme condition by assuming an exclusive development of one set of glands, and the higher mammalian condition by an exclusive development of the other. The significance of this was later fully appreciated by Klaatsch ('92), on the discovery by him of both kinds of glands in the peculiar mammary pouches of artiodactyl ungulates. On

[1] A more moderate position on this subject has recently been taken by Jenkinson ('00).

page 365 of his paper he speaks of a fundamental correspondence between the artiodactyl ungulates and the monotremes in this respect.

Here we may notice the opinion of Wilson and Hill ('97, p. 579): "We do not believe that in the long run it will be found possible to maintain the essential dissimilarity of the mammary glandular organ in monotremes." This appears to be the more appropriate attitude.

With regard to the results of Osborn, Hubrecht quotes, among other statements, the following one, which he interprets as indicating polyphyletic origin: "All stem mammals were related in their double succession (of teeth), in their dental formula, and in their primitive molar form. These features point not to a succession, but to a unity of ancestry of the monotremes, marsupials, and placentals." [1]

This involves the broader question as to how convergence of type ought to be interpreted in the Mammalia; for, in addition to the results of Osborn, those of Wilson and Hill ('97) confirm convergence in dentition, those of Gegenbaur ('86) and Klaatsch ('92), convergence in the mammary glands, those of Klaatsch ('92, '95), finally, convergence in the accessory mammary apparatus. All of these suggest unity of ancestry.

If there were no convergence of type in the structures under consideration, Huxley's hypothesis would immediately become untenable, because it would then be necessary to assume a polyphyletic origin. But if we admit convergence, the chances are equally divided between genetic succession and polyphyletic origin. In order to prove the latter, however, it would be necessary to trace the converging structures back to a pre-mammalian stage. In other words, it would be necessary to prove that in progressive development certain structures diverged in character before the mammalian condition was instituted; because if any structure diverged from a type which was still mammalian, the latter would be regarded as also prototherian. None of the above-named structures have as yet been traced to a non-mammalian type.

[1] Osborn ('93, p. 20).

Finally, Hubrecht mentions the results of Klaatsch in connection with polyphyletic origin. He quotes from Klaatsch as follows: "Dadurch wird man zu der Annahme gedrängt, dass die Hufthiere sich ganz direkt an jene oben dargestellte Urform der Säugethiere anschliessen, deren hypothetische Vertreter man als Taschenthiere oder Bursalia von den Beutelthieren oder Marsupialia unterscheiden kann. Es wird denkbar, dass die Hufthiere niemals ein Marsupialstadium durchliefen."[1]

If we follow Klaatsch throughout the course of his paper, we find that he recognizes a primary condition of the mammary apparatus consisting of paired mammary pouches lodging the mammary glands. Out of these are formed independently the incipient marsupium of monotremes and the perfect marsupium of marsupials. In the artiodactyl ungulates these pouches show no signs of marsupium formation; they are converted into the tubular teat cavities. He accordingly concludes that the artiodactyl ungulates have not passed through a marsupial stage (Marsupialstadium).

Although this is doubtless a true interpretation, it cannot be regarded, as Hubrecht suggests, as pointing to polyphyletic origin; for it is not our object in contemplating polyphyletic origin to prove that, for example, the artiodactyl ungulates have not passed through a marsupial stage, but that they have not passed through a metatherian stage. The results of Klaatsch confirm that which Huxley, notwithstanding the meagerness of his evidence, perceived, namely that the marsupium is not a transitional character but a special character of marsupials.[2]

We may again refer to the opinion of Wilson and Hill ('**97**, p. 579). Concerning the mammary pouches of Klaatsch they speak as follows: "Such a rudimentary or primitive condition must have been characteristic of the common stock of both Metatheria and Eutheria, and was only a marsupial one in the sense that Echidna is now marsupial." From this it is clear that they do not regard Klaatsch's results as at all indicative of polyphyletic origin.

[1] Klaatsch ('**92** p. 369).

[2] Huxley ('**80**, p. 656).

There are still to be noticed certain phases of opinion which chiefly concern the relationships of the Monotremata. In a recent paper by Osborn ('99), to which reference has already been made, we find the Monotremes separated off from the marsupials and placentals, and assigned an independent origin on a basis of their distinctness of organization. A similar view has also been expressed by Seeley ('96, '99).

Under the circumstances this view has been a most natural one. The tendency of recent research has been essentially towards the revelation of placental characters in the Marsupialia (Wilson and Hill ('97), Hill ('97)), on the one hand, and the revelation of sauropsidan (theriodont, Seeley) characters in the Monotremata (Semon ('94), Seeley ('96, '99), van Bemmelen ('98, '99, '00), Smith ('99), Sixta ('00), Hochstetter ('96), Ziehen ('97)). Thus the two groups have been naturally regarded as genetically distinct. It is probable, however, that in assigning a separate origin to them we overestimate their distance apart: in the first place, on account of the deceptive mask of placental characters which the Marsupialia, especially those of Australia, have assumed; and in the second place, because, while diligent search has been made for sauropsidan characters in the Monotremata, little has been done towards a recognition of the prototherian characters of marsupials. That the latter field is not unproductive may be seen from the discovery by Broom ('97), in a fœtal marsupial, of a distinct coracoid comparable to that of the Monotremata, and the recent results of McClure, showing that the numerous variations of the postcaval and related veins in the opossum (*Didelphys virginiana*) are all modifications of a ground type which Hochstetter has shown to be characteristic of the embryonic Monotremata.[1] Moreover, we should not lose sight of the familiar osteological characters which marsupials and monotremes have in common.

Reviewing the evidence as a whole, there seems to be no adequate reason for abandoning Huxley's hypothesis. Many of the facts which have recently come to light are rather confirmatory than otherwise, and many others, which have been

[1] These results were kindly communicated to me by Professor McClure.

regarded as antagonistic, are open to a different interpretation. Since it has not been definitely disproven, and especially since no other view has been advanced which explains all of the facts of the case as well, we may justly regard Huxley's theory as entitled to first consideration, even at the present day.

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For references to papers of Owen, Caldwell, Selenka, and Semon, on the marsupial allantois, see Hill (**'97**, p. 438).

THE THEORIES OF THE ORIGIN OF THE ANTARCTIC FAUNAS AND FLORAS.

ARNOLD E. ORTMANN.

WHILE preparing a report on the fossil Tertiary invertebrates of Patagonia collected by the Princeton expedition, the writer was led to collect the literature on the subject of the resemblance of the southern faunas and floras (of South America, South Africa, Australia, and the Antarctic islands), and was very much surprised by the vague and sometimes incorrect representations of the existing theories relating to this fascinating zoögeographical question. Many authors do not quote their predecessors at all, while others refer to them only in a very general way, occasionally misstating their views or giving incorrect or defective quotations. I have, therefore, tried to collect everything that has been written on this topic, and think it will be worth while to give here a condensed report on the subject.

One of the first to call attention to the resemblance of southern life, in this case to that of the flora, and certainly the first to advance a theory, was Hooker.[1] He is of the opinion that we could possibly explain the fact of the existence of identical plants in southern lands widely distant from each other by the assumption that there was once a connection of these parts by land. This theory, first expressed very cautiously, and at that time much disputed, was again more energetically propounded by Hooker,[2] and, in the last paper, with reference to the Darwinian view of the origin of species.

In the course of time this theory was almost forgotten, at

[1] Hooker, J. D. *The Botany of the Antarctic Voyage of H. M. Discovery Ships Erebus and Terror* (*Flora Antarctica*), Pt. ii (1847), p. 211.

[2] Hooker, J. D. Introductory Essay to the Flora of New Zealand (1853), pp. xxiii ff.; and On the Flora of Australia; its Origin, Affinities, and Distribution, *Botany of the Antarctic Expedition*, Pt. iii, vol. i (1859), pp. xvii and civ.

least it is not referred to by the next writers to be mentioned, whom we should regard as the founders of the theory of the Antarctica. The first of them is Ruetimeyer.[1] He states distinctly that we should take a part of the present faunas of South America, South Africa, and Australia for remnants of an old fauna that spread over a larger extent of the Antarctic continent, and that this Antarctic continent was the center of origin of a peculiar Antarctic fauna.

Practically the same idea — but without reference to Ruetimeyer — was set forth a little later by Hutton[2]; that is to say, he also assumed the former larger extension of the Antarctic continent, and its connection with the southern ends of the present continents.

In 1875 Gill,[3] relying on his studies on fishes, constructed his Eogæa, which was apparently conceived as a large continental mass, embracing Africa, South America, and Australia; but no mention is made of the Antarctica entering it.

In opposition to all these theories, which construct land bridges, where there is now deep water, Wallace,[4] consistent with his views on the permanence of land and oceans, entirely repudiates these opinions, and believes that the faunal elements common to the southern continents are remnants of a formerly more extensive distribution, and have been pushed into the southern ends of the land by the competition with other animals.

In favor of this view, Hutton[5] abandons his first theory of a connection by an Antarctic continent. But he still maintains that there must have been a connection between Australia and South America, and he constructs a bridge across the mid-Pacific, assuming a large Pacific land mass, which was

[1] Ruetimeyer, L. *Ueber die Herkunft unserer Thierwelt.* Basel, 1867.

[2] Hutton, F. W. On the Geographical Relations of the New Zealand Fauna. *Trans. New Zealand Inst.*, vol. v (1873); reprint in *Ann. Mag. Nat. Hist.*, Ser. 4, vol. xiii (1874).

[3] Gill, T. On the Geographical Distribution of Fishes, *Ann. Mag. Nat. Hist.*, Ser. 4, vol. xv (1875).

[4] Wallace, A. R. *The Geographical Distribution of Animals*, vol. i (1876).

[5] Hutton, F. W. On the Origin of the Fauna and Flora of New Zealand, *New Zealand Journ. Sci.*, January, 1884; reprint in *Ann. Mag. Nat. Hist.*, Ser. 5, vol. xiii, June, 1884.

joined, on the one side, to Australia and New Zealand, and, on the other, to Chili.

Von Ihering [1] takes up again the Antarctic communication, but at the same time he accepts, at least in part, Hutton's Pacific continent. According to him, a large land mass extended from South America across the Antarctic regions to Australia, from whence it continued into the Pacific continent, and even communicated with Asia (Archinotis). The Pacific continent was not directly connected with Chili.

While all these writers expressed their opinions on the Antarctica only in a very general way, Forbes [2] was the first to give it a more definite shape by drawing a map of it. He constructs his Antarctica by raising the land to about the present two thousand fathoms line, which results in an enormous extension of the Antarctic land masses.

In opposition to this, Hedley [3] restricts the Antarctica considerably, and admits only narrow connections of it with the other continents. He does not think that New Zealand was ever joined to the Antarctica by land, and does not believe in Hutton's Pacific continent, although a part of the Pacific islands were once connected with Australia and New Zealand. Of the latter relations he gives a map in his second paper.

Finally, Osborn [4] gives a map of the possible extent of the Antarctica by raising the land to the 3040 meters line. This attempt resembles somewhat that of Forbes, but shows a

[1] Ihering, H. von. On the Ancient Relations between New Zealand and South America (*Trans. New Zealand Inst.*, vol. xxiv, 1891), and Die Ameisen von Rio Grande do Sul (*Berlin. entomol. Zeitschr.*, Bd. xxxix, 1894). See also *Science*, v, December 7, 1900.

Von Ihering has referred to this subject in numerous other papers, and it is extremely difficult to collect all of them, since a large number have been published in out-of-the-way places. Lists of them have been given by himself in Engler's *Botanische Jahrbücher*, Bd. xvii (1893), p. 9, and *Science*, v.

[2] Forbes, H. O. The Chatham Islands; their Relation to a former Southern Continent (*Roy. Geograph. Soc. Suppl.*, vol. iii, 1893); abstract: Antarctica, a supposed former southern continent (*Natural Science*, vol. iii, 1893).

[3] Hedley, C. Considerations on the Surviving Refugees in Austral Lands of Ancient Antarctic Life (*Proc. Roy. Soc. N. S. Wales*, 1895), and A Zoögeographic Scheme for the Mid-Pacific (*Proc. Linn. Soc. N. S. Wales*, 1899).

[4] Osborn, H. F. The Geological and Faunal Relations of Europe and America during the Tertiary Period, etc., *Science*, April 13, 1900.

tendency to restrict the boundaries of this continent to reasonable dimensions, thus approaching Hedley's ideas.

Other writers have only added new facts to the material already at hand that favors the assumption of a former continental connection of the southern regions, and they have all accepted the general idea of Hooker and Ruetimeyer, without making any material change in it; therefore I do not consider it necessary to mention them here.

We may sum up all theories advanced, and put them into a table in the following way:

I. Theories assuming a land connection between the respective parts. This general idea was first expressed by Hooker (1847). It has been accepted by all subsequent writers except Wallace.
   1. The land bridge is placed across the present Antarctic continent, first by Ruetimeyer (1867) and by Hutton (1873). It was accepted by Von Ihering, Forbes, Hedley, Osborn.
      (*a*) Forbes constructs his immense Antarctica (1893).
      (*b*) Hedley restricts it to reasonable limits (1895).
      (*c*) Osborn takes an intermediate standpoint (1900).
   2. Gill constructs his Eogæa, a continent uniting Africa, South America, and Australia, but leaving out the Antarctica (1875).
   3. Hutton connects Australia and South America by his mid-Pacific continent, but denies the existence of an Antarctic connection (1884).

II. Theory of Wallace (1876) rejecting any land connections whatever between the respective parts.

I do not want here to go into any further detail, since my only purpose is to give an account of the existing theories with proper references, and to classify them according to their contents. But I may state here that in the forthcoming report on the Patagonian fossils mentioned above, I shall accept Hooker's general idea, as well as Ruetimeyer's Antarctica theory, with the restrictions put upon it by Hedley, and thus we may call it *the Hooker-Ruetimeyer-Hedley theory.*

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THE GENERIC NAMES MYRMECOPHAGA AND DIDELPHIS.

OLDFIELD THOMAS.

THERE have recently appeared in America two papers on these generic names, the one in this journal, by Mr. J. A. G. Rehn,[1] and the other, criticising the first, by Dr. J. A. Allen.[2] The points raised in both appear to me to need further discussion, especially with regard to the somewhat ready manner in which the species usually quoted as the type of each name is thrown aside as unrecognizable.

I. MYRMECOPHAGA.

With regard to *Myrmecophaga tridactyla*, which, if determinable, would admittedly be the type of the generic name, Mr. Rehn, while discussing Linnæus's references to Seba and Ray, altogether ignores the very first quotation of all, that to Marcgrave ("Tamandua-guacu, Marcgr. bras. 225"). On examination Marcgrave's animal proves to be beyond all question the great ant-eater of Brazil, and on the general principle of taking the first important reference as the basis for Linnæus's names we must clearly accept the great ant-eater as the type of the genus Myrmecophaga.

Linnæus's words, "*macula nigra a pectore versus latus ducta*" and "*cauda lata*," are also diagnostic of the great ant-eater, mistaken as are his statements about the digits and mammary formula.

It is unfortunate that the specific name, dating from the tenth instead of the twelfth edition of the *Systema Naturæ*, must be *tridactyla* instead of the familiar *jubata;* but even this

[1] *Am. Nat.*, vol. xxxiv, p. 575, July, 1900.

[2] *Bull. Am. Mus. N. H.*, vol. xiii, p. 185, October, 1900.

is a lesser evil than the transference of Myrmecophaga to the Tamanduas and the dubbing of the great ant-eater with a new generic name.

Dr. Allen says that while differing about Didelphis, he agrees with Mr. Rehn in regard to Myrmecophaga, but as he seems also not prejudiced (as I am) against dismissing old names as unrecognizable, and has probably not looked up the vital reference to Marcgrave, I do not feel justified in accepting Mr. Rehn's conclusions, even when backed by so great an authority as he is.

As a result I claim that *Myrmecophaga tridactyla* Linn. should be the name for the great ant-eater, Uroleptes and Cyclopes remaining as before for the other genera of the family.

II. DIDELPHIS.

In this case Dr. Allen most rightly refutes the necessity asserted by Mr. Rehn for calling all the large opossums Sarigua instead of Didelphis, but I fail to be convinced as to his application of the specific name *marsupialis* to the Virginian opossum. This name *marsupialis* hangs primarily on Seba's figure, and both authors claim that the latter is unrecognizable, Dr. Allen going on to make the remarkable statement that it is "not an American animal, but a species of Phalanger from Amboyna." It is true that Seba said his animal was from Amboyna, but even at that date mistakes could be made as to locality, and no one familiar with Phalanger, its general appearance, dentition, or mammary formula, could for one moment suppose that Seba's figure and description were based on a member of that genus. Among the whole of the Mammalia the peculiar arrangement of the mammæ is alone absolutely diagnostic of a Didelphis, nor have I any doubt what opossum it is meant to represent.

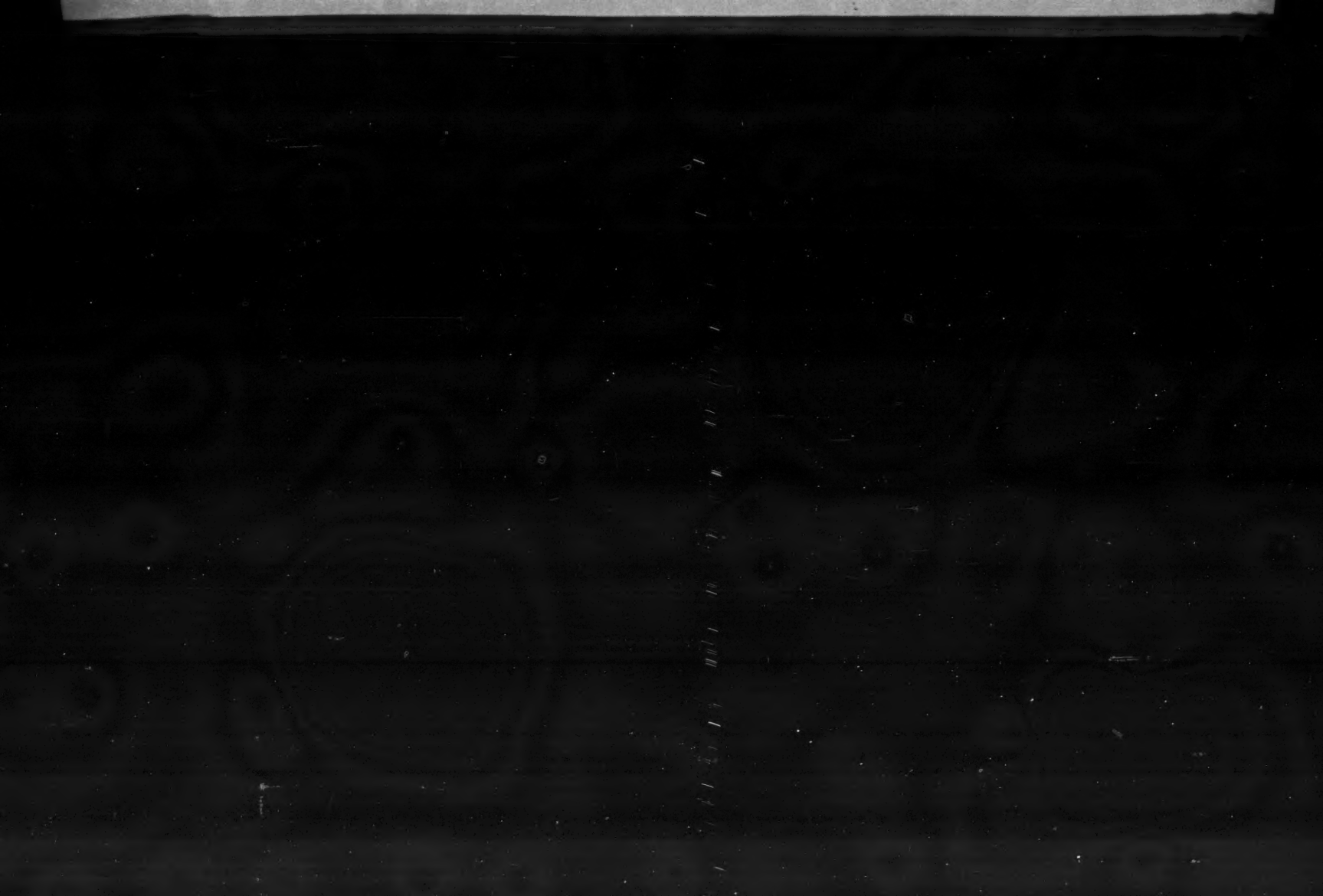
Seba's South American animals nearly all came, as was natural, from Guiana, and the figure will perfectly suit the ordinary dark opossum of northeast South America, for which Dr. Allen has used the name *D. karkinophaga*.

This conclusion, if accepted, will have the double advantage of retaining the familiar term *virginiana* for the Virginian opossum, and abolishing so jaw-breaking a name as *karkinophaga*.

In the necessity of renaming Philander I am compelled to acquiesce, though I may express a regret that in giving the name Caluromys Dr. Allen has departed from the modern practice of restricting the ending -mys to members of the Rodentia.

But of his transference of the species *cinereus* and *alstoni* from Marmosa to Caluromys I find it more difficult to approve, for the points that he mentions as allying them to the latter are all found in different degrees in one or other of the larger species of Marmosa, including *M. murina*, while neither *cinereus* nor *alstoni* present those which are more truly characteristic of Caluromys. The general shape of the skull of the latter, the small rounded molars, the great sabre-like canines, the curiously shaped lower jaw, and many other characters make up an *ensemble* to which, as it appears to me, neither of the species referred to shows any real approximation. I should therefore consider them both as members of the genus Marmosa.

British Museum, Natural History.



THE APPLICATION OF DIDELPHIS MARSUPIALIS LINNÆUS.

JAMES A. G. REHN.

RECENTLY Dr. J. A. Allen published a paper, "Note on the Generic Names Didelphis and Philander" (*Bull. Amer. Mus. Nat. Hist.*, XIII, pp. 185–190), in which he takes exception to several statements recently published in this journal (XXXIV, pp. 575–577) by the present writer. A very hasty examination of Dr. Allen's paper convinced me that some of his conclusions must have been hastily formed, as they show a lack of detail.

A more painstaking scrutiny has disclosed several interesting points in regard to the references cited by Linnæus under his *Didelphis marsupialis;* as, like Dr. Allen, I have changed my views regarding the recognition of this name.

To quote from Dr. Allen: "It is a recognized rule of nomenclature that a name applied to a composite group, whether specific or generic, must be conserved for some one of its components when the group is later subdivided." With this I agree perfectly, and, as Dr. Allen argues, think we should give each reference cited under the name a close examination, the description being too indefinite to furnish anything. This Dr. Allen has done, but not as thoroughly as it should be.

To take the references mentioned above, they are as follows:

Philander Seb. Mus., I, p. 64, t. 39.

Opossum Tyson, act., 290, p. 1565.

Carigue Laët, Amer., 551.

Carigueija brasiliensibus Marcgr. bras., 222; Pis. bras., 323; Jonst. quadr., 136, t. 36.

Maritacaca Pis. bras., 323; Ray quadr., 182.

Tlacuatzin Hernand. mex., 330.

Concerning the first, the Philander of Seba, we find something of interest even if it does not affect the whole. An

examination of this work shows that if Dr. Allen had examined it closer he would have modified his statement that "the Philander of Seba . . . is not an American animal, but a species of Phalanger from Amboyna." The first part of the description of this animal is quoted from Valentino (*Amboinensis Animal.*, p. 273), and while it very probably relates to a species of Phalanger as Dr. Allen states, the latter part of the text (which is that of Seba) undoubtedly refers to an opossum. Such statements as "Caput, canino simile, longum protendit rostrum, acutisque dentibus . . . dorsum longis pilis, setaceis, atro spadiceis, hispidum est . . . cauda, longa, squamis rhomboideis tota tegitur," surely do not refer to a Phalanger. Seba makes the statement that Valentino had made a great error in describing the animal as he did; accordingly he gives his idea of the same, which, with the plate (undoubtedly a Didelphis), shows that Seba had nothing but an opossum in mind.

The second, Tyson's work, has been already closely examined by Dr. Allen, and nothing further can be said regarding it. The third reference, the Carigue of De Laët, I cannot examine, and therefore will pass over, as very likely the animal is a South American opossum which would not be identifiable.

The Carigueija of Marcgrave, Piso, and Jonston is an opossum of South American origin, but both the description and the locality are too indefinite to be considered.

The fifth, the Maritacaca of Pisonis, I cannot examine, but Ray has quoted it in its entirety, from which the same conclusions as the foregoing would be entertained.

The last, the Tlacuatzin of Hernandez (*Anim. Mex.*, p. 330, 1651), is an opossum which represents the form inhabiting the southern end of the tableland of Mexico, the Cordilleras, and Vera Cruz, as Mr. Nelson (*Science*, N.S., VIII, p. 897) has pointed out regarding *Spermophilus variegatus* Erxleben, which was based on an animal described by Hernandez. To quote from Mr. Nelson: "At the time when Fernandez made his observations the main area of Spanish occupation in Mexico was the southern end of the Mexican tableland, about the valley of Mexico, and thence eastward across the plains of Puebla, throughout the Cordillera to the hot lowlands of Vera Cruz."

According to the evidence set forth, the point is raised, — should Tyson's reference be given precedence over that of Hernandez?

Disregarding the dates of the references (that of Hernandez being forty-seven years older), we will proceed with the work by elimination.

The opossum "from Virginia" was separated by Kerr in 1792, while the southern Mexican animal, which, if it has been separated, can only be either *californicus* or *breviceps* Bennet, which were not described until 1833. The only other species of the genus which is found anywhere near the locality in question is *D. aurita*, which has not (to my knowledge) been recorded north of Guatemala. The elimination of Tyson's reference by the *D. virginiana* Kerr leaves us only the reference of Hernandez as the base of *Didelphis marsupialis* Linnæus.

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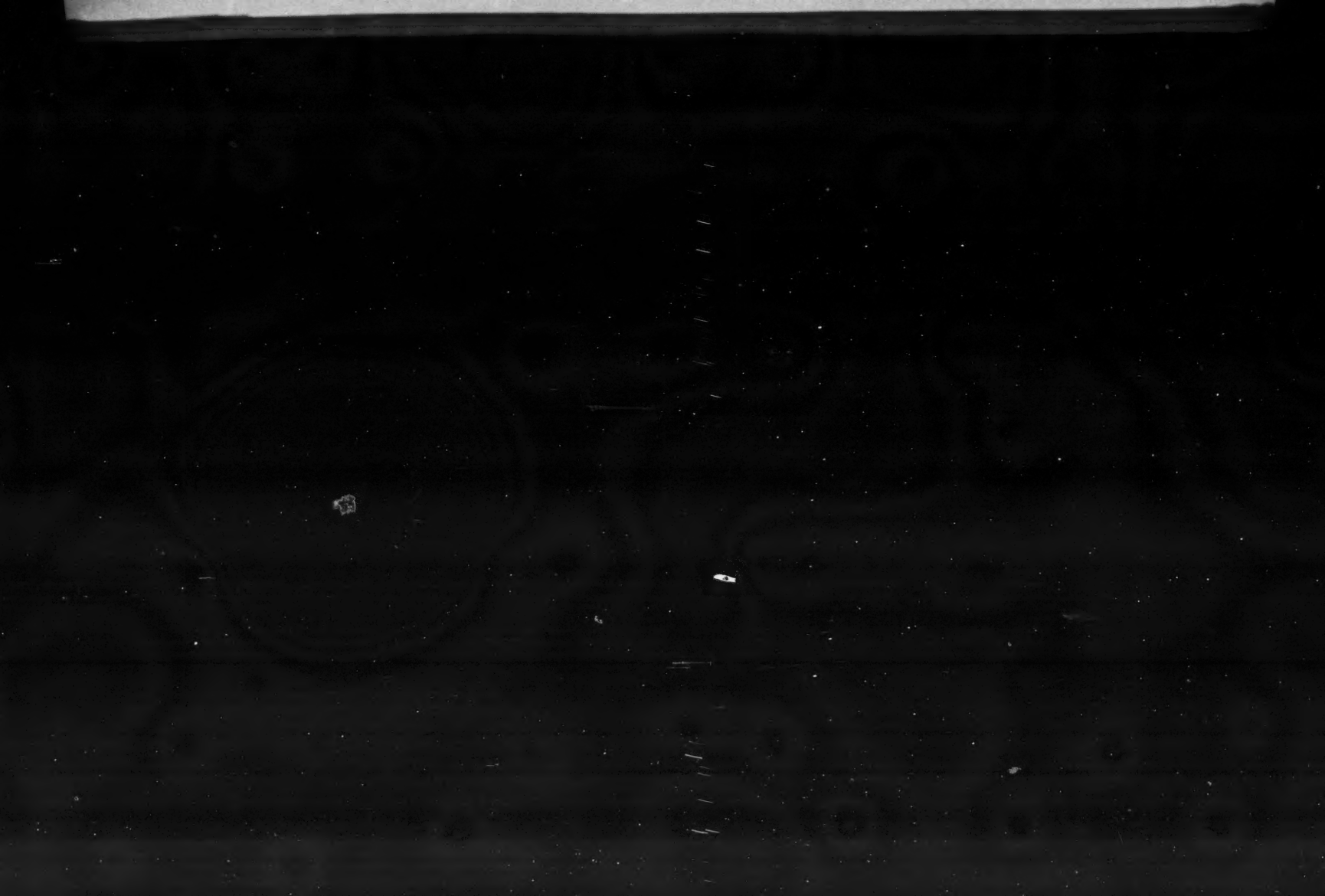

THE SNAKES OF NEW YORK STATE: AN ANNOTATED CHECK LIST.

EDWIN C. ECKEL.

No paper on the ophidian fauna of this state has appeared since Baird's "Serpents of New York," published in the *Seventh Annual Report on the Condition of the State Cabinet, Albany*, 1854. That which is now presented is merely a list of those species which have been mentioned more or less definitely as occurring within our limits.

The notes which I have added are of two classes. In the case of species whose presence within the state is doubtful, I have given the authority for their inclusion. In this connection I have endeavored to give credit, for the introduction of new species into our faunal lists, to those to whom it is due.

My own observations on the snakes of this state have been confined largely to that portion of the state which I traverse during my geological field work. With this area and with its fauna I am fairly well acquainted, having spent my summers for the past twelve years within it. I have, therefore, added a few notes upon the occurrence and abundance of the various species in southeastern New York. This area, as the term is used here, has geological rather than geographical boundaries. Roughly defined, it includes the counties of Orange and Rockland, on the west of the Hudson, and those of Westchester, Putnam, and the southern half of Dutchess, on the east of the river. It is an area of crystalline rocks, bordered on the north by a usually well marked depression based on limestones and shales. In one case at least, the herpetology seems to be affected by the geology. The rattlesnake is rarely seen outside of the Highlands, while the copperhead is abundant in the great Cambro-Silurian lowland which adjoins the Highlands on the north. The ophidian fauna of the region is rich

in both species and individuals, while in the Catskills, not far away, there is a notable scarcity of snakes.

I have adopted the terminology and classification of Cope, as set forth in his *Crocodilians, Lizards, and Snakes of North America*, though a note under the heading of *Eutænia sirtalis* expresses my dissent from his method of handling the subspecies of that group.

1. *Carphophiops amœnus* (Say).
2. *Diadophis punctatus* (Linn.).

   So far as my observation goes, very scarce in the southeastern counties.
3. *Heterodon platyrhinus* Latreille.

   Very common in sandy regions in Orange County and southern Westchester County. I have never encountered the melanistic form which has been variously described as *H. niger* and *H. p. niger*, but Cope notes a specimen from Scarboro, Westchester County, and there is now in the New York Zoölogical Park a living specimen taken in Sullivan County.
4. *Liopeltis vernalis* (De Kay).

   More common, I believe, in Orange County than east of the Hudson.
5. *Zamenis constrictor* (Linn.).

   A very common species, both relatively and absolutely, in southeastern New York.
6. *Coluber vulpinus* (B. & G.).

   Jordan (*Manual Vertebrates Northern United States*, eighth edition, p. 195) gives the range of this species as "Massachusetts to Kansas, and north." Cope, however (*Crocodilians, Lizards, and Snakes of North America*, p. 831), states that it is not known from east of Illinois, and I have been unable to find any record of its occurrence in or near New York.
7. *Coluber obsoletus obsoletus* Say.

   Occurs in Orange County (and probably east of the Hudson), though much scarcer than *Zamenis constrictor*.
8. *Pityophis melanoleucus* (Daudin).

   Included as a possible straggler over our southern border.
9. *Osceola doliata triangula* (Boie).

   A rather common snake in Orange County; less abundant, I believe, east of the Hudson.
10. *Osceola doliata clerica* (B. & G.).

    Cope quotes a specimen (U. S. Nat. Mus., No. 1407) whose locality is given as "(?) New York." As this state is far beyond the most

northern range of the subspecies, so far as any other records go, the label may be considered as in error.

11. *Ophibolus getulus getulus* (Linn.).

Baird ("Serpents of New York," 1854) states that "the chain snake is quite maritime in its northern distribution, being rarely found in the Northern States, except near the coast." De Kay had mentioned its occurrence on Long Island. In a "Catalogue of Reptiles and Fishes, from St. Lawrence County, procured for the State Cabinet of Natural History by Franklin B. Hough" (*Fifth Annual Report on Condition of State Cabinet, Albany*, 1852), I find that Dr. Hough collected specimens of this species from Rossie, St. Lawrence County, and that he quotes it as "of common occurrence in this portion of the state." These specimens cannot now be found, but I am inclined to accept the record, as John Gebhard, then Curator of the State Cabinet, had too thorough a knowledge of the ophidian fauna of the state to have allowed an obvious error to stand in the catalogue.

12. *Natrix fasciata sipedon* (Linn.).

Abundant in all the counties of southeastern New York. The normal ground color here is dark grayish to black. I have never seen individuals of the brownish or yellow-brown color described by some authors, and shown by casts at several prominent museums.

13. *Natrix fasciata erythrogaster* (Shaw).

Cope quotes a specimen (U. S. Nat. Mus., No. 9984) as from Westfield Falls, Connecticut. This is far to the north and east of the usual range of the subspecies, and may be an error in the label.

14. *Natrix leberis*.

I have never seen individuals of this species in southeastern New York, though much of my field work has been in localities which would seem to furnish a highly favorable environment.

15. *Storeria dekayi* (Holbrook).

This and the next species are abundant in southeastern New York, though both are so inconspicuous and retiring as readily to escape observation. As late as 1898 I have found a specimen of *S. occipitomaculata* on New York Island.

16. *Storeria occipitomaculata* (Storer).

Described by De Kay as extra-limital, this species was included in the fauna of the state by John Gebhard, Jr. (*Fourth Annual Report on Condition of State Cabinet, Albany*, p. 23, 1851), as specimens had been obtained by Dr. Fitch in Washington County. Three years later than this publication Baird, in his "Serpents of New York" (*Seventh Annual Report on Condition of State Cabinet, Albany*, p. 124, 1854), "formally introduced" the species as "an inhabitant of New York."

17. *Eutænia saurita* (Linn.).

In Westchester and Putnam counties this species appears to be even more abundant than *Eutænia sirtalis*. It is rarely found out of the immediate vicinity of water, though it is not so truly aquatic in its habits as is *Natrix fasciata sipedon*. On being alarmed this latter serpent will usually go below the surface, for a time at least. *Eutænia saurita*, on the contrary, when flushed from its place of concealment in the reeds or grass along the shore, will remain on the surface, not going far from the bank of the stream or pond, and watching for a favorable opportunity to regain the shore.

18. *Eutænia brachystoma* (Cope).

The single specimen on which this species is founded was taken at Franklin, Venango County, Pennsylvania. The species may, therefore, be found within our limits.

19. *Eutænia sirtalis graminea* (Cope).

No specimens are recorded from this state, and I have never seen an individual of *E. sirtalis* even approaching the coloration of this subspecies as described by Cope, but as specimens are described from both Ohio and Massachusetts, the subspecies is here included.

20. *Eutænia sirtalis ordinata* (Linn.).

21. *Eutænia sirtalis sirtalis* (Linn.).

Both this subspecies, and that immediately preceding, are common in southeastern New York. My own observations upon the various forms of *Eutænia sirtalis* occurring in New York have led me to feel that the subspecific grouping proposed by Cope is not entirely satisfactory.

In addition to those here listed we have in this state, I believe, at least two forms of equal rank with *E. s. ordinata* and *E. s. sirtalis*. Whether any of these forms of *E. sirtalis* occurring in New York are sufficiently distinct to be given subspecific rank is still, I think, an open question.

I had hoped to be in a position, before the publication of this paper, to discuss this subject in a more definite manner, but I have not been able to accumulate sufficient material to do so. This being the case, I have used Cope's grouping and terminology in this list.

22. *Eutænia sirtalis obscura*.

The type specimen of this subspecies was obtained at Westport, New York.

23. *Ancistrodon contortrix* (Linn.).

Occurs in swamps and low grounds in Orange and Dutchess Counties, but scarcer in the Highlands. Most of the many snakes annually killed as "Copperheads" are individuals of the species *Heterodon platyrhinus*, *Ophibolus doliatus triangulus*, or even *Natrix fasciata sipedon*.

24. *Sistrurus catenatus catenatus* (Raf.).

Described by De Kay as extra-limital, but added by Gebhard (*Sixth Annual Report on Condition of State Cabinet, Albany*, p. 22, 1853), as specimens had been sent in from Genesee County. There appears to be no recent definite record of their occurrence in that region.

25. *Crotalus horridus* (Linn.).

Still occurs in Orange and Rockland Counties, but very rare and possibly extinct east of the Hudson in this state. Cope notes a specimen collected in 1878 at Katonah, Westchester County; and I have been informed that one was killed in 1887 near White Plains.

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